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# Sand eels (*Ammodytidae*) in the south-western North Sea; their biology and fishery

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# Sand eels (*Ammodytidae*) in the south-western North Sea; their Biology and Fishery

## INTRODUCTION

FIVE species of sand eel have been recorded from the North Sea – *Ammodytes marinus* Raitt, *A. lancea* Cuvier, *A. lanceolatus* Lesauvage, *A. immaculatus* Corbin, and *Gymnammodytes semisquamatus* (Jourdain). The name *A. tobianus* L. appears to have been given to a mixture of two species and has tended to be dropped by some modern workers (see Jensen, 1941); where it is used in the literature, it is nearly always the equivalent of *A. lancea*. *A. immaculatus* is very rare in the southern North Sea and as far as is known there is only one record of it in this area (Meyer-Waarden, 1959). *A. lancea* is primarily an inhabitant of sandy bays and is scarce offshore. The remaining three species are, however, common offshore, but one of them, *A. marinus*, occurs in much greater concentrations than the others and it is this species that forms the basis of the fishery.

Previous work on sand eels has been mainly of a systematic nature concerned with both the adults and larvae. A review of systematic work on adults is given by Richards et al. (1963) and on the larvae by Einarsson (1951) and Macer (1965). Aspects of the fishery have been dealt with by Roessingh (1957), Bertelsen and Popp Madsen (1958) and Meyer-Waarden (1959 et seq.), amongst others. A general biological study has been made by Cameron (1959 *a*).

The fishery is an 'industrial' one, the sand eels being crushed and dried to yield meal and oil, and it takes place in two main areas, near the continental coast (mostly off Germany and Denmark) and between the north Norfolk coast and the south-western edge of the Dogger Bank; it is the fishery in the latter area that has been the subject of the present investigations (Figure 1). These began in 1960 as a general study of the biology of sand eels in this area, with special reference to the fishery. Concern was expressed by some English fishermen who felt that the sand-eel fishery might harm other fish stocks, but an English fishery was contemplated by others, since the fish occurred near to the English coast, and especially adjacent to the Humber. Such a fishery would have involved difficulties with the size-limit regulations, and it did not then materialize, though there have been a few landings of sand eels at Hull by foreign vessels. In 1964 there was renewed interest by some English fishermen in starting a sand-eel fishery, and some trial landings were made at Grimsby, but these were not found to be sufficiently profitable.

## MATERIALS AND METHODS

THE work was carried out from the Ministry's research vessel *PLATESSA*, a 90-foot wooden M.F.V. The nets used were the same as those employed by the commercial boats and were purchased at Esbjerg in Denmark; a description of this type of net has been given elsewhere (Anon. 1957 *a*, Anon. 1960 *a*). In all, fourteen research cruises were made, five in 1960, seven in 1961 and two in 1962. From each haul the catch was separated into species and the quantity of each was noted. Representative samples of all species were then measured, to the nearest half-centimetre for sand eels and to the nearest centimetre for other species. The stomach contents of the latter were examined to determine the extent of feeding on sand eels.

For each sand-eel species a sample, consisting of five fish from each half-centimetre group, was preserved in 90% alcohol and brought back to the laboratory, where the otoliths, stomachs and suitable ovaries were extracted, and the sex and stage of maturity noted. Later, the stomach contents were examined and the age of the fish determined from the otoliths, which were read (immersed in xylene) using reflected light.

When the fish were examined after preservation it was found that they had nearly always shrunk slightly. In converting length distributions to age this shrinkage was corrected by applying the otolith readings of a half-centimetre length group to the next group above. For example, ages from preserved fish measuring 10 cm would be applied to the fish measuring 10·5 cm (fresh) at sea. Further details of methods will be found in the text.

In the account which follows, the area investigated (Figure 1) has normally been divided into two, with the boundary along the deep-water channel of the Outer Silver Pit. The area to the north is referred to as the Dogger and that to the south, between the 20 fathom contour and the Norfolk and Lincolnshire coasts, as South of Dogger. In the case of *A. marinus*, the latter area has been subdivided into the Norfolk Banks (the area between the Leman and Indefatigable Banks inclusive) and the Dowsing (including the Outer Dowsing and Haddock Bank areas).

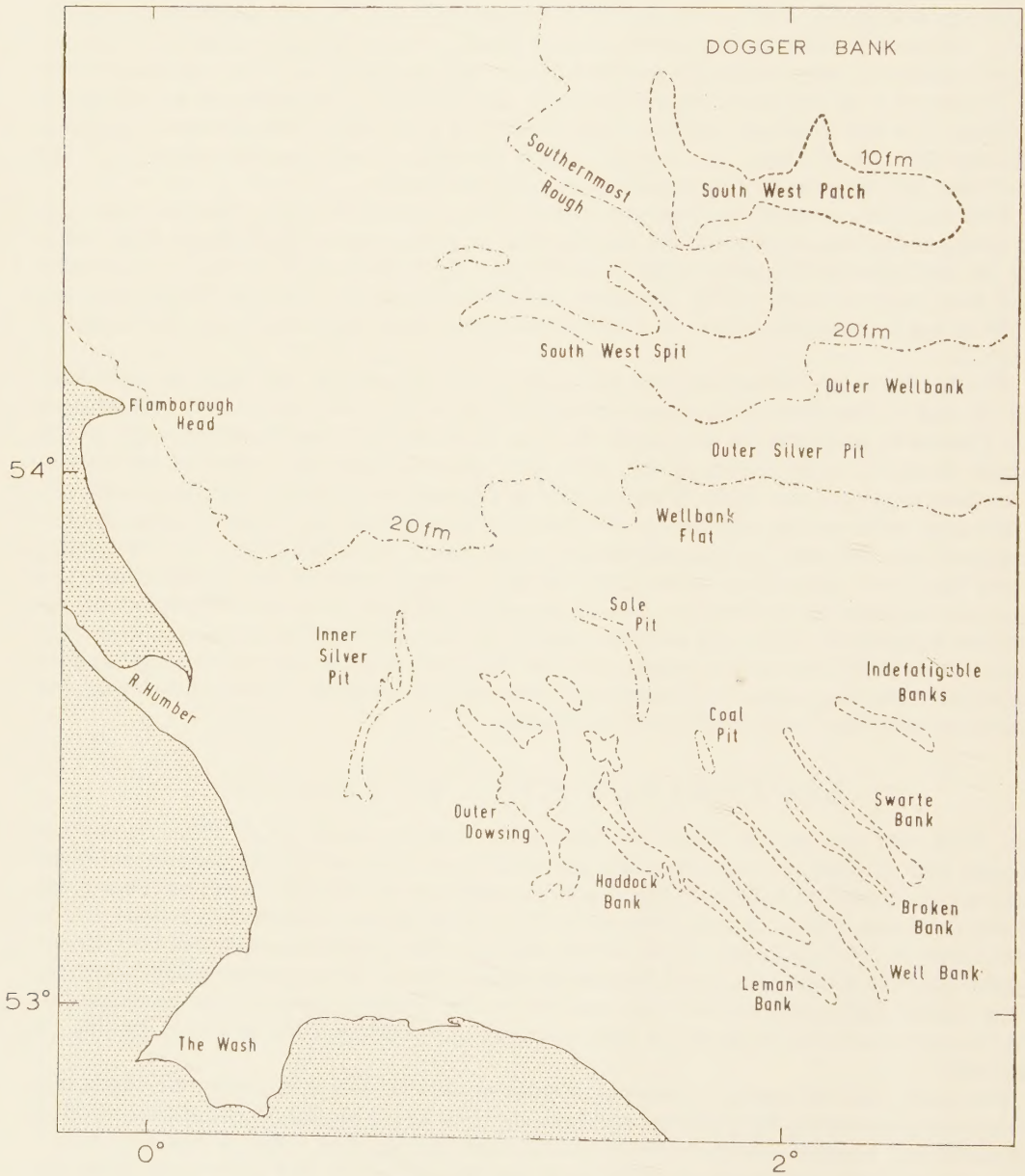


FIG. 1. *The south-west Dogger Bank and the Norfolk Banks.*

# PART I – BIOLOGY

## DISTRIBUTION AND ABUNDANCE

SAND eels tend to be concentrated in well-defined areas; this is particularly true of *A. marinus*, and it is on the large concentrations of this species that the fishery primarily depends.

In the areas investigated the concentrations followed two patterns, one to the north of the Outer Silver Pit and the other to the south. To the north, the areas of maximum concentrations occurred near the 20 fathom contour of the south-west Dogger Bank, whilst to the south they were on the tops of the Norfolk Banks in depths of twelve fathoms or less. This is demonstrated in Table 1, where mean catches per hour for the relevant depths in the two areas are shown for the three species. To the north of the Outer Silver Pit, more than 90% of each species was taken in 15–20 fathoms. To the south, a high percentage of *A. marinus* and *A. lanceolatus* occurred in less than 12 fathoms but this was not so with *G. semisquamatus* in which the majority, 63·9%, were in water deeper than 12 fathoms.

The distribution and abundance of sand-eel species in the areas investigated are shown in Figure 2; grounds to the north and south of the Outer Silver Pit are shown separately for convenience of presentation. The choice of station positions was influenced by the nature of the bottom, since rough ground has to be avoided when using the sand-eel trawl. For example, the commercial fishing ground near the Southernmost Rough is an area of sand between the Rough itself and the 20-fathom contour. Thus the abundance of sand eels on the Rough itself is not so well known, since it is unsuitable for the gear. However, on the occasions when the boat has strayed on to this area, and the net has remained intact, few sand eels have been caught. Towards the Outer Silver Pit side of the ground the restricted nature of the sand-eel shoals is even more striking. If the trawl is shot in the deep water of the Pit and is then towed on to the bank (or vice versa), the catch in the cod-end can be seen to be sharply divided between almost pure sand eel from the shallow water, and flatfish and whiting from the deeper water.

The two parts of Figure 2 emphasize the difference between distributions in different areas. No sand eels were caught on a line of stations across the top of the Dogger Bank, whereas they were caught on the tops of the Norfolk Banks, though the depths over the latter are generally about 5 fathoms less than those over the Dogger Bank. More work would be needed to prove the absence, or at least scarcity, of sand eels from the top of the Dogger, since only a single haul was made at each of these stations. Most of the other stations, both on the edge of the Bank and to the south of the Outer Silver Pit, were sampled at least three times. As can be seen from Figure 2, *A. marinus* is by far the most numerous species. The largest catch, an estimated 305 000 fish for a one-hour tow on the Southernmost Rough ground in January 1962, is not included since the other areas were not sampled at the same time. Though not so abundant, *A. lanceolatus* has a wider distribution; the largest catch – 4 374 fish/hour – was made on the Dowsing Shoal. *G. semisquamatus* is more localized than the previous two species, and its main centres of distribution were: Southernmost Rough, Dowsing, and Indefatigable/Swarte Bank areas. Despite its restricted distribution, the highest number recorded – 4 891 fish/hour on the Southernmost Rough – was greater than that found for *A. lanceolatus*. *A. lancea* was only rarely found, as follows: Leman Bank (one fish), Well Bank (one fish), Haddock Bank (four fish). It is primarily an inshore species and is usually the dominant form in beach-seine hauls. No specimens of *A. immaculatus* were taken, although it has been recorded from the North Sea (Meyer-Waarden, 1959).

Of the total number of sand eels caught on all cruises 94·5% were *A. marinus*, 2·9% *A. lanceolatus* and 2·6% *G. semisquamatus*.

The three principal characteristics of sand-eel distributions are (a) the fish occur in shoals; (b) the shoals are restricted to definite areas, in depths which are different to the north and south of the Outer Silver Pit; and (c) the areas of maximum concentration differ between the species.

With regard to (c), it has been shown that whereas *A. marinus* and *A. lanceolatus* occurred

Table 1. *Abundance of sand-eel species related to depth in catches from R.V.* PLATESSA

| | North of Outer Silver Pit | | | | | | South of Outer Silver Pit | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth | 15–20 fm | | | >20 and <15 fm | | | <12 fm | | | >12 fm | | |
| Species | *A. marinus* | *A. lanceolatus* | *G. semisquamatus* | *A. marinus* | *A. lanceolatus* | *G. semisquamatus* | *A. marinus* | *A. lanceolatus* | *G. semisquamatus* | *A. marinus* | *A. lanceolatus* | *G. semisquamatus* |
| Mean No. per hr. | 8 130 | 157 | 255 | 763 | 12 | 3 | 9 242 | 382 | 84 | 301 | 74 | 149 |
| % of species | 91·4 | 92·9 | 98·8 | 8·6 | 7·1 | 1·2 | 96·8 | 83·8 | 36·1 | 3·2 | 16·2 | 63·9 |
| No. of hauls | | 57 | | | 31 | | | 35 | | | 31 | |

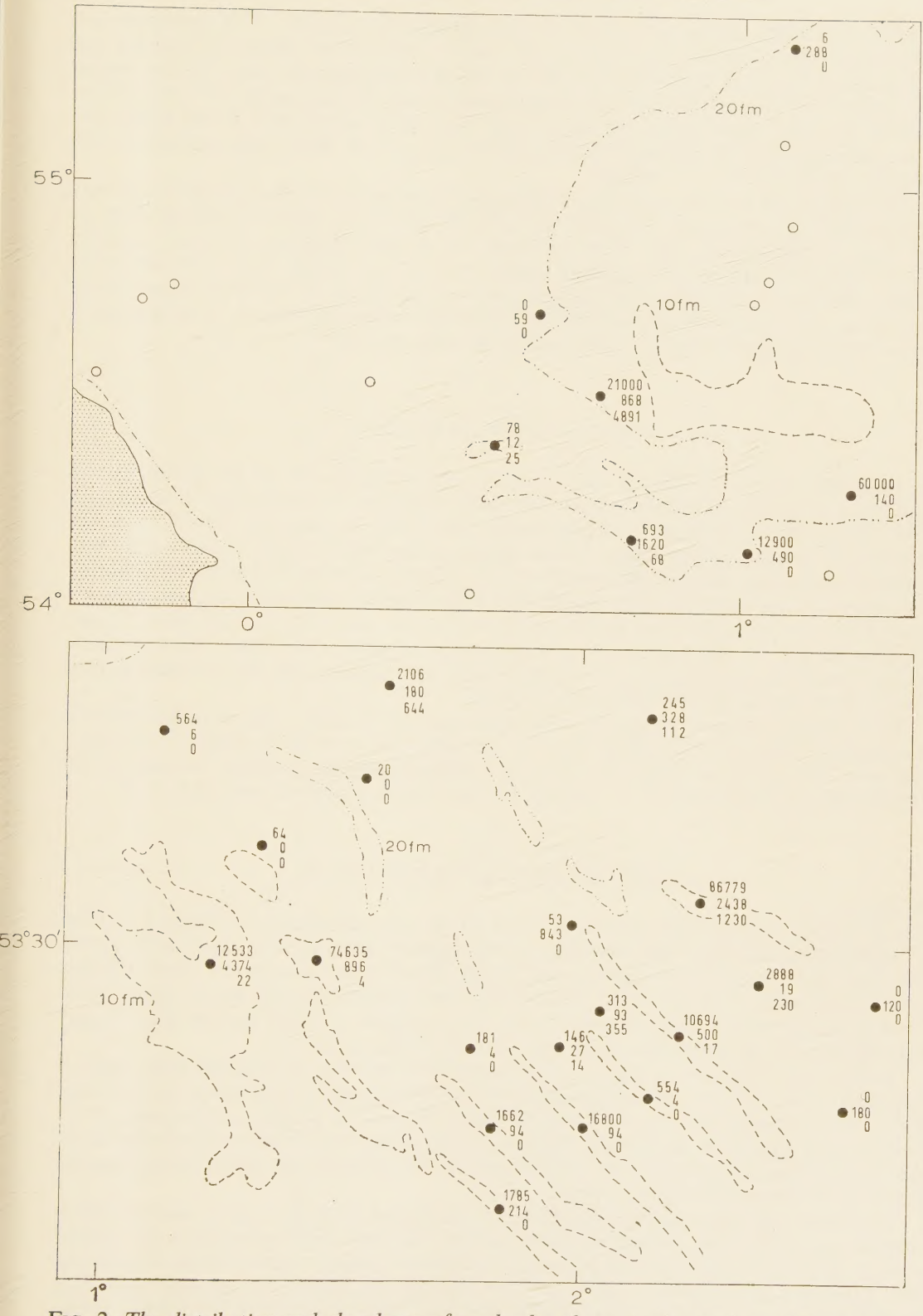


FIG. 2. *The distribution and abundance of sand eels: above, in the south-west Dogger area; below, south of the Dogger. The numbers are the maximum caught per hour at each position (black circles); upper number* – A. marinus; *middle number* – A. lanceolatus; *lower number* – G. semisquamatus. *Open circles indicate hauls made but no sand eels caught.*

in greatest numbers on the tops of the Norfolk Banks, the majority of G. *semisquamatus* were found off the banks. The latter species and *A. marinus* both feed on plankton (see below) and this partial separation may help to avoid competition for food. (*A. lanceolatus* is a predator, taking, in the main, other sand eels.) Although this separation could not be detected on the Dogger Bank, the shoals may have been mixed only in the trawl. The hauls were generally of an hour's duration, so in the two or three miles covered several separate shoals might well be caught.

The reasons for the restricted nature of the distributions have been discussed elsewhere (Macer 1965). It is probably connected with particle size of the substrate and its effect on the fishes' burrowing habit (an escape reaction). In addition, particles which are too large or too small may hinder gill ventilation whilst the fish are buried. Thus sand eels avoid muddy areas (e.g. Outer Silver Pit) and concentrate in sandy areas, the latter usually being ones where tides and wave action would be expected to scour the bottom, so giving rise to coarse sand (e.g. edge of Dogger Bank, tops of Norfolk Banks).

## AGE DETERMINATIONS

As previously stated the otoliths were used for age determination in all species. It was found that, in general, the growth zones were quite distinct in *A. marinus* and *A. lanceolatus* but tended to be less clear in *G. semisquamatus*; examples are shown in Plate 1. It can be seen that in the latter species (Plate 1 *d*) the opaque zones (which appear white) are not well separated by hyaline zones (black), and about 22% of the otoliths were classified as 'doubtful' with respect to age determination, though they were assigned to an age-group and included in the data. The proportions of 'doubtfuls' for *A. marinus* and *A. lanceolatus* were 9% and 5% respectively. In the case of *G. semisquamatus*, especially, the length measurements usually formed distinct modes corresponding to the year-classes, and this provided a good check on age determinations (Petersen's method).

In the absence of marked growth differences between the sexes, they have been treated as a single population in the growth data. For all species an assumed 'birthday' of January 1 was used. The system of using age-groups was adopted, so that 'O-group' referred to fish from hatching to December 31. A 'I-group' fish was thus in its second year, and so on.

## LENGTH, AGE AND GROWTH

*A. marinus*

The percentage length compositions of fish from all areas are shown in Figure 3 and the principal age-groups have been indicated. It was apparent from the first year's work (1960) that there were marked differences in the length distributions of sand eels from different areas; hence modes in a combined distribution from different grounds (as in Figure 3) do not necessarily refer to different year-classes. In particular, it could be seen that Dogger Bank fish tend to be larger than those taken farther to the south.

In 1961 the differences in length were investigated more fully by sampling from April to August on three grounds – the Southernmost Rough area on the Dogger Bank, the Haddock Bank/Dowsing area, and the Indefatigable Bank (Figure 1). Length distributions of *A. marinus* from these areas are given in Figure 4. It was found that mean length was highest in the Southernmost Rough fish and lowest in the Haddock Bank fish, whilst those from the Indefatigable Bank were intermediate.

The percentage age compositions are shown in Figure 5 for three areas, each of which includes one of the three grounds mentioned above. The most striking feature is the relative scarcity of the 1958 year-class on all grounds. They are poorly represented as II-group in 1960, III-group in 1961 and IV-group in 1962. Though the reasons for this poor year-class are not known, it is perhaps worth noting that very large numbers of *A. marinus* larvae (up to 2 000 per $m^2$ below surface), probably from a different population, were caught during larval plaice surveys in the Southern Bight in 1958.

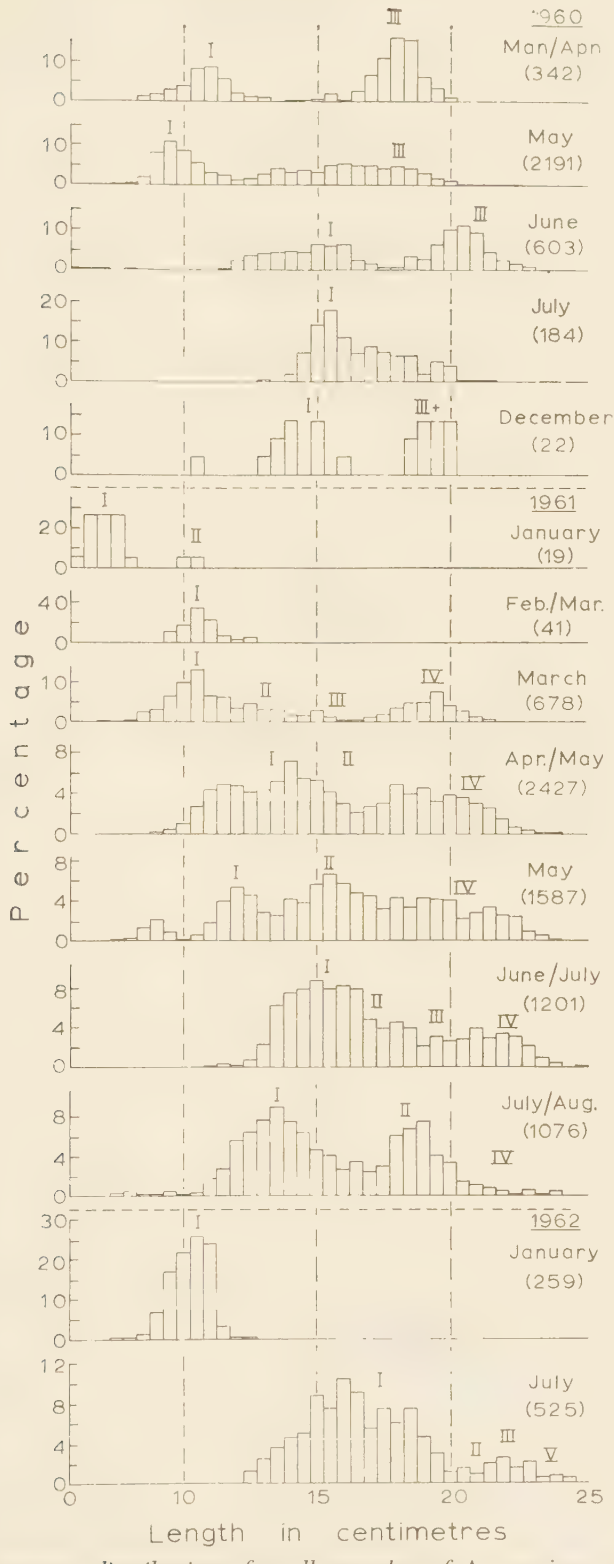


FIG. 3. *Length-frequency distributions for all samples of* A. marinus *for each cruise. The numbers measured are given in parentheses and the principal age-groups are shown by Roman numerals.*

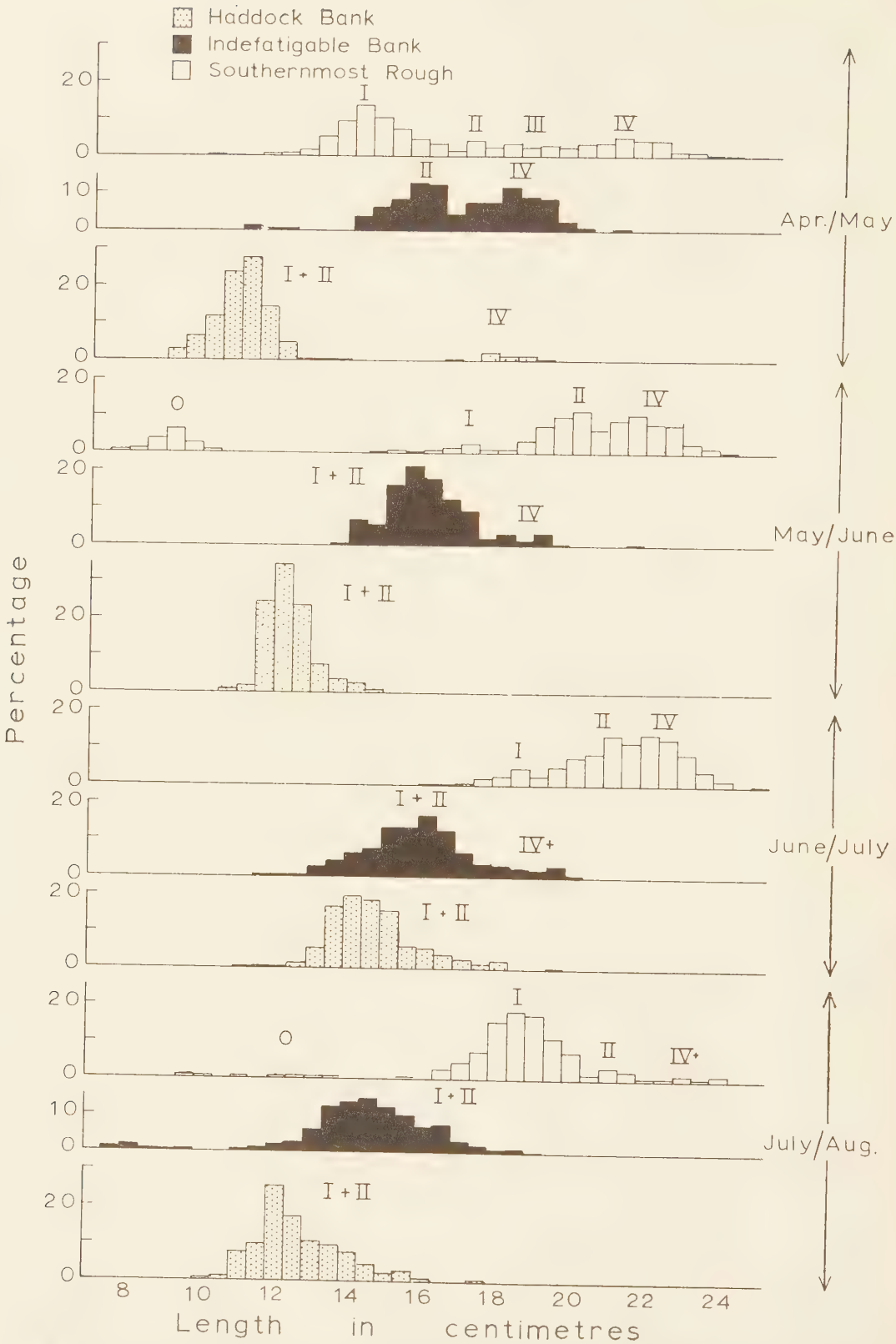


FIG. 4. *Length-frequency distributions for* A. marinus *from three grounds in* 1961. *Roman numerals indicate age groups.*

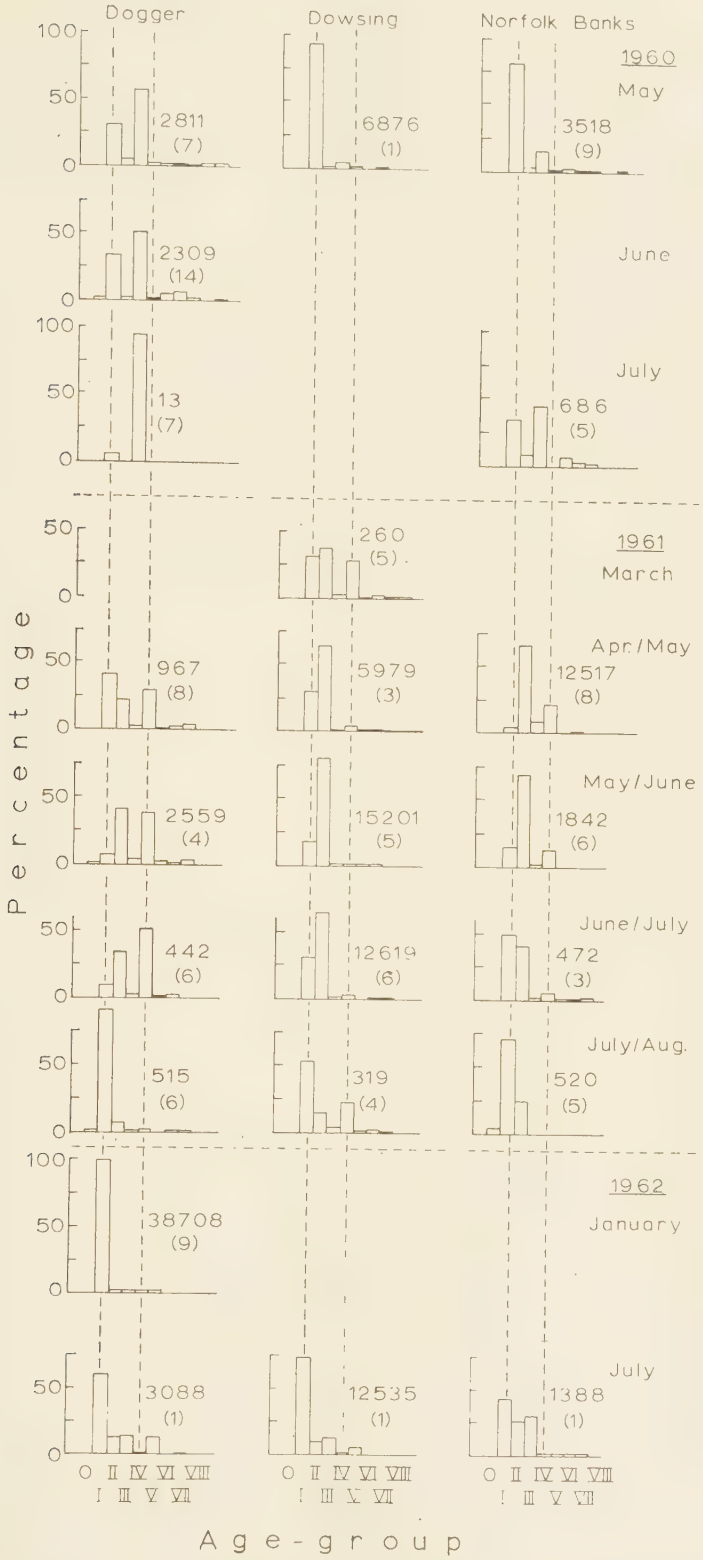


FIG. 5. *Age compositions of* A. marinus *from three areas on each cruise. The numbers represent the mean numbers caught per hour and, in parentheses, the number of hauls.*

In 1960 two year-classes (1957 and 1959) are conspicuous, but whereas the 1959 year-class (I-group) outnumbers the 1957 year-class (III-group) on the Dogger, the reverse tends to be true on the other grounds. In 1961, these same two year-classes (now II- and IV-group) continue to be conspicuous but towards August tend to be overshadowed by the 1960 year-class (I-group). One sample was obtained from the Dogger Bank in January 1962 and I-group fish (1961 year-class) formed over 99% of the total. By July this proportion had fallen to 59·4%, compared with 72·0% in the Haddock/Dowsing area and 42·4% on the Norfolk Banks.

The oldest reliably-aged fish taken was a IX-group.

In addition to determining mean lengths by measurements of the fish themselves, growth in previous years was calculated by measuring the widths of the growth zones in the otoliths and finding the relation between total otolith width and length of fish (Figure 6). One year's growth was taken to include an opaque zone and the hyaline zone at its periphery. Most of the points on the graph represent the means of twenty observations, but at the extremes of the length range of each age there were fewer examples. Otoliths of doubtful age were not included. It was found that growth in width of the otolith was related to length of fish and also to age, so that, at a given length, older fish tended to have wider otoliths, though not invariably so.

Table 2 sets out mean lengths in various months for year-classes from 1957 to 1961 on the three grounds, and the data for the last three year-classes are shown graphically in

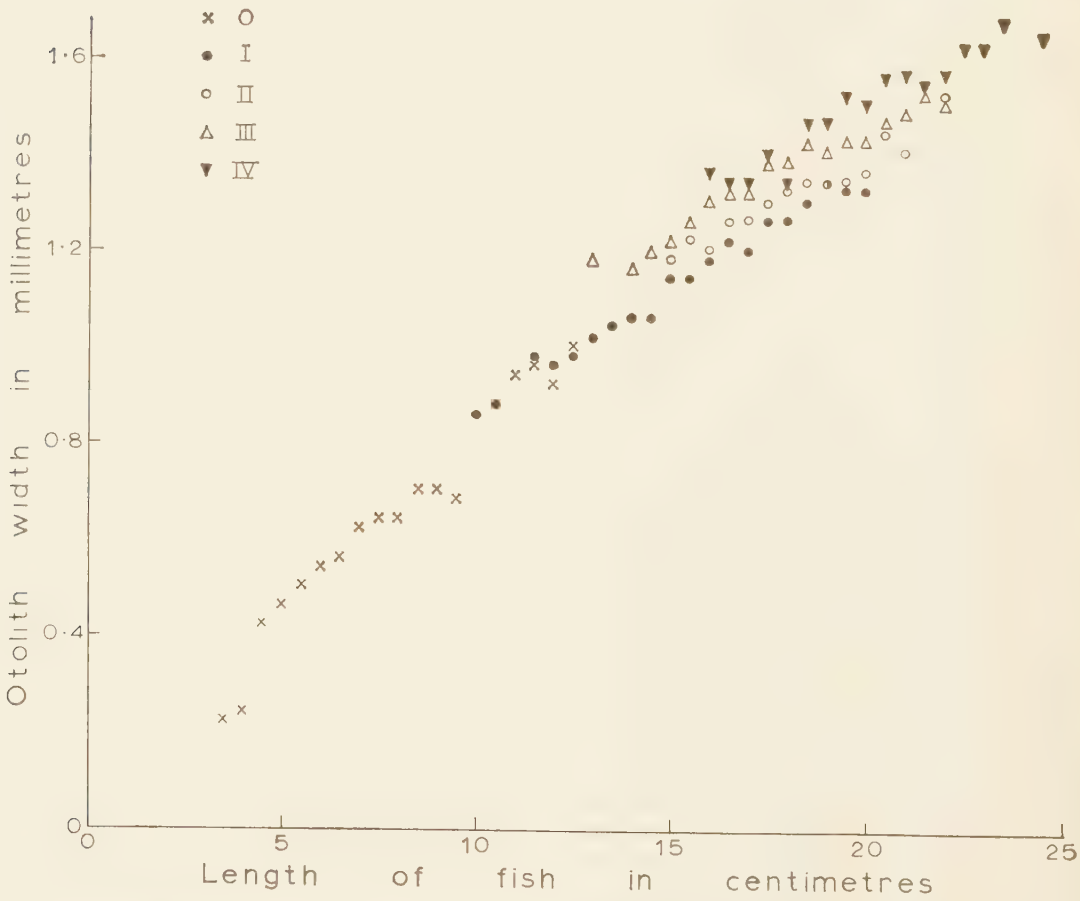


FIG. 6. *The relation between otolith width and length of fish for different age-groups in* A. marinus.

Table 2. A. marinus. *Mean lengths of year-classes (cm) and numbers measured (lower figure)*

| Ground | Year-class | 1960 | | | 1961 | | | | | | 1962 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Jan. | May | June | Jan. | Mar. | Apr.–May | May–June | June–July | July–Aug. | Jan. | July |
| Southernmost Rough | 1957 | | ↑ | 20·4 | | | 21·0 | 21·8 | 22·4 | 22·8 | | 22·9 |
| | | 0 | | 227 | 0 | 0 | 159 | 173 | 120 | 6 | 0 | 24 |
| | 1958 | | | 16·8 | | | 20·0 | 21·3 | 20·8 | 23·0 | | 23·0 |
| | | 0 | | 5 | 0 | 0 | 17 | 19 | 8 | 2 | 0 | 2 |
| | 1959 | 9·3* | NS | 15·6 | 17·0* | | 17·9 | 19·5 | 20·6 | 21·0 | | 20·7 |
| | | 223 | | 117 | 223 | 0 | 142 | 176 | 117 | 19 | 0 | 26 |
| | 1960 | – | | | 9·3* | | 14·2 | 16·6 | 18·0 | 18·5 | | 20·2 |
| | | | | 0 | 288 | 0 | 448 | 31 | 31 | 212 | 0 | 25 |
| | 1961 | – | | – | – | | | 8·9 | | 11·5 | 10·2 | 18·2 |
| | | | ↓ | | | 0 | 0 | 72 | 0 | 9 | 259 | 114 |
| Haddock Bank | 1957 | | 15·4 | ↑ | | | 18·1 | | 16·9 | | | 18·3 |
| | | 0 | 16 | | 0 | 0 | 8 | 0 | 5 | 0 | 0 | 9 |
| | 1958 | | 14·5 | | | 13·3 | | | 17·3 | 14·0 | | 18·0 |
| | | 0 | 2 | | 0 | 2 | 0 | 0 | 6 | 3 | 0 | 1 |
| | 1959 | 8·8* | 9·6 | NS | 10·7* | 10·4 | 11·2 | 12·4 | 14·6 | 13·7 | | 15·5 |
| | | 226 | 256 | | 132 | 120 | 74 | 80 | 237 | 29 | 0 | 21 |
| | 1960 | – | | | 8·7* | 8·5 | 10·3 | 11·6 | 14·1 | 12·5 | | 15·1 |
| | | | 0 | | 110 | 4 | 60 | 31 | 109 | 160 | 0 | 17 |
| | 1961 | – | – | | – | | | | | | | 14·6 |
| | | | | ↓ | | 0 | 0 | 0 | 0 | 0 | 0 | 122 |
| Indefatigable Bank | 1957 | | 16·5 | ↑ | | ↑ | 18·6 | 17·9 | 18·5 | | ↑ | 18·5 |
| | | 0 | 129 | | 0 | | 38 | 29 | 27 | 0 | | 1 |
| | 1958 | | 15·3 | | | | 18·3 | 18·0 | 16·5 | | | 17·2 |
| | | 0 | 18 | | 0 | | 20 | 2 | 6 | 0 | | 3 |
| | 1959 | 9·1* | 9·8 | NS | 11·8* | NS | 15·8 | 15·7 | 15·7 | 16·0 | NS | 16·8 |
| | | 124 | 231 | | 122 | | 118 | 185 | 144 | 86 | | 48 |
| | 1960 | – | | | 9·0* | | 15·3 | 15·6 | 15·0 | 14·2 | | 16·5 |
| | | | 0 | | 94 | | 4 | 44 | 96 | 204 | | 42 |
| | 1961 | – | – | | – | | | | | 8·3 | | 15·7 |
| | | | | ↓ | | ↓ | 0 | 0 | 0 | 12 | ↓ | 68 |

* derived from otolith measurements; lower figure refers to number of otoliths measured.
NS = Ground not sampled.

Figure 7. The values which have been derived by back-calculation from otolith measurements are indicated by the symbols $L_1$ or $L_2$ above the points.

Two interesting anomalies are apparent in Figure 7. The first of these is that the 1959 year-class (open circles) on the Indefatigable and Haddock Banks put on only a very small growth increment in 1960, compared with the two subsequent year-classes and with the same year-class on the Southernmost Rough. The result of this poor growth was that, in 1961 and 1962, the 1959 and 1960 year-classes (the latter shown by solid circles) had similar mean lengths. This is illustrated further by the otolith photographs in Plate 1 (*a* and *b*). These two sets of otoliths are from fish caught at the same time in 1961 on the same ground; *a* is from a 1960 year-class fish, *b* 1959 year-class. It is apparent that the second opaque growth zones are markedly different, that in *b* being about half the width of *a*. The reasons for the poor growth are not known but are presumably related to a shortage of food. This shortage could not have applied to the fish in their first (O-group) year or to the Dogger fish.

The second noteworthy point about the growth data shown in Figure 7 is that some decreases in mean length were recorded in 1961 on the Indefatigable and Haddock Banks. In some cases the decreases are small and could be due to small sample size, but this does not seem to be the case with the Haddock Bank decrease. If it were due to some kind of sampling error, the Southernmost Rough data would be expected to show similar decreases

but none are evident. Two possibilities which might account for the phenomenon are an emigration of larger fish or an immigration of smaller ones. The larger fish might, for example, tend to migrate to a spawning ground; it is known that the Southernmost Rough is such an area (Macer 1965) and it may be significant that there was no decrease in mean length there. However, two objections to this explanation are that the 1959 year-class on the Indefatigable Bank showed no decrease in mean length, and in addition the gonads showed no external signs of maturing at this time. An influx of smaller fish might be due to prolonged recruitment, and there was some evidence of this (see below).

The length data in Figure 7 and Table 2 indicate that the main growing period is between January and August. In 1961 no samples were obtained after August, but on the Southernmost Rough, where the data seem to be the most reliable, the growth curve appeared almost to have reached its peak in this month. The start of the season's growth cannot be precisely

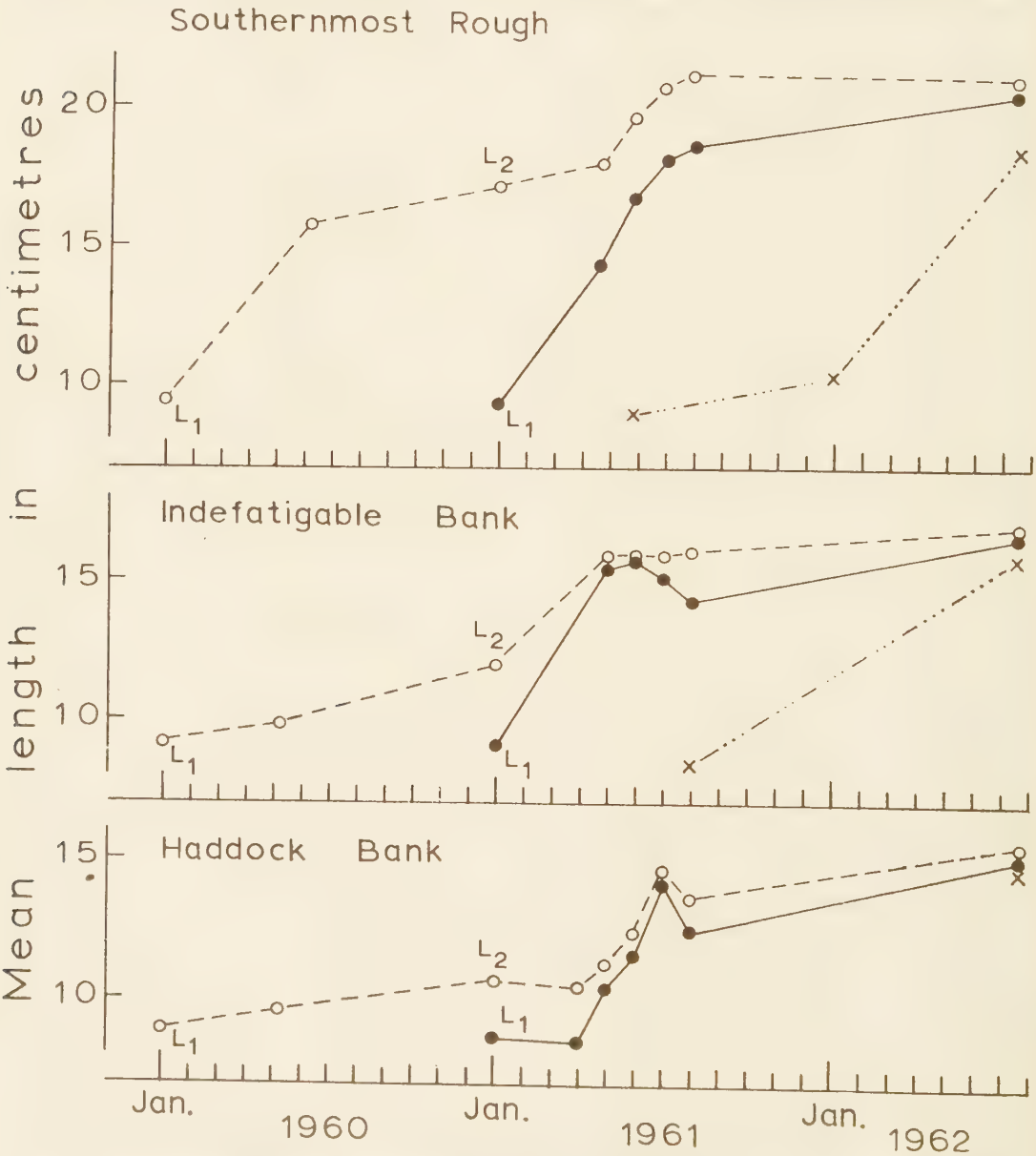


FIG. 7. *The growth of different year-classes of* A. marinus *on three grounds.* ○1959 *year-class:* ●1960 *year-class:* ×1961 *year-class.*

stated, since no data are available between January and the end of April for this ground. On the Haddock Bank, there was no increase in mean length until after the end of March.

*A. lanceolatus*

The length compositions of this species are shown in Figure 8, which includes fish from the same areas as for the previous species, except that some from the Texel area are included in the July/August 1961 histogram. Since the length range is much greater than in *A. marinus*, centimetre instead of half-centimetre groups have been used in the diagram. The largest fish taken was 38 cm – much larger than the maximum length attained by the other sand-eel species which occur in the area.

The otoliths (Plate 1 *c*) were usually easy to interpret. There was much variation in the width of the first growth zone, almost certainly reflecting the prolonged spawning season. The age compositions of fish from the Dogger and South of Dogger grounds (Figure 9) show that longevity is no greater than it is in *A. marinus*, despite the fact that a greater length is attained. This was unexpected, since mature specimens of *A. lanceolatus* feed largely on sand eels and predators usually have a longer lifespan than their prey. In marked contrast to *A. marinus*, the 1958 year-class dominated in both areas in 1960 and 1961, although it was relatively more important in the Dogger area than in areas to the south, always forming more than 50% of the total numbers in the former area. In 1962, the 1960 year-class was predominant in the southern areas, but no samples were obtained from the Dogger. The two areas differ in age composition in two respects: (a) no I-group fish were taken on the Dogger; (b) the 1956 year-class was stronger than the 1957 year-class south of the Dogger but not on the Dogger.

The increase in proportion (and also absolute abundance) of V-group fish in July/August 1961 in the areas south of the Dogger is noteworthy and may be due to immigration of larger individuals of this year-class, since there was also a relatively large increase in mean length. It is possible that these comparatively large predacious fish move about freely in search of their food – chiefly other sand eels (see section on feeding).

Plots of mean length against age for the populations in the two areas in 1961 (Figure 10) show that the Dogger fish tend to be larger than those taken farther south, though the differences were not so marked as in the *A. marinus* data. Mean lengths in all years are set out in Table 3 and the Texel specimens are also included. The latter have a lower mean length than those from the other areas except for the I-group, though there are no data on this age-group for the Dogger area.

In the months in which samples were obtained, the greatest monthly growth increment recorded was 3·3 cm for the I-group in July 1961 south of the Dogger. A year later this group had increased its mean length by only 3·3 cm, so growth had slowed considerably. As previously mentioned, there was a relatively large increment (2·2 cm) among the V-group in July in this area.

*G. semisquamatus*

Figure 11 shows the percentage length distributions of fish of this species from all cruises. Fairly distinct modes were usually apparent and this was a considerable help in determining the age of the specimens. The maximum length attained by this species is similar to that reached by *A. marinus*, and the largest fish taken measured 23·5 cm.

Though a comparatively large proportion of the otoliths were classed as 'doubtful' with respect to age, it is considered that with the aid of the length data reliable age determinations were made. Examining the age structure of the Dogger and South of Dogger fish (Figure 12), some differences are apparent. In 1961, for example, the 1958 year-class predominated on the Dogger Bank, as compared to the 1959, and later the 1960, year-classes in the other area. The dominant year-class was again different in the two areas in 1962. The oldest specimen taken was a VII-group, a similar age to that reached by the other two species.

Once again, the data on mean length at age (Figure 13 (1961 only), Table 4) showed that this tended to be higher on the Dogger Bank than it was in the more southerly areas, although the greatest difference amounted to only 1·7 cm. The monthly increments recorded in 1961 were very small; as with *A. lanceolatus*, the samples were obtained in the spawning season, which may not coincide with the period of maximum growth.

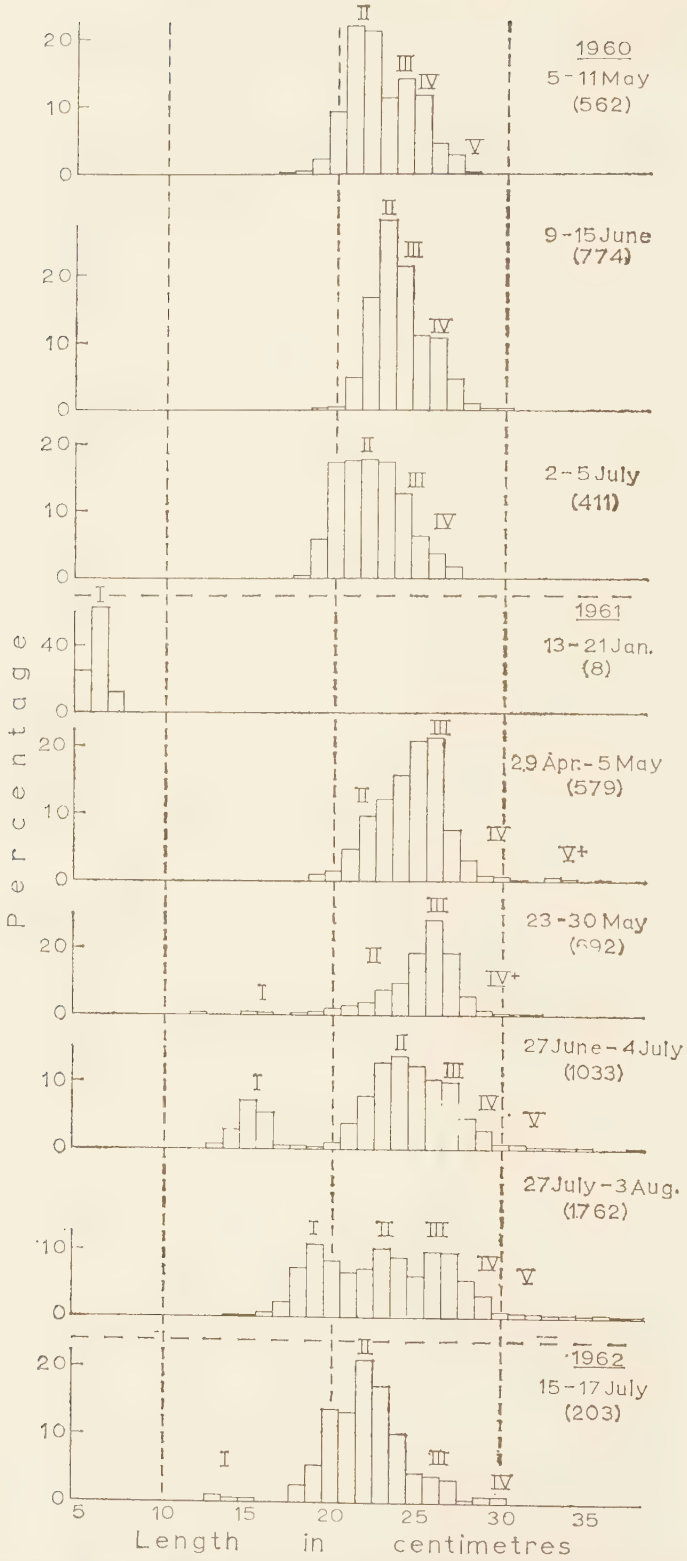


FIG. 8. *Length-frequency distributions of all samples of* A. lanceolatus *for each cruise. The numbers measured are given in parentheses and the principal age-groups are shown by Roman numerals.*

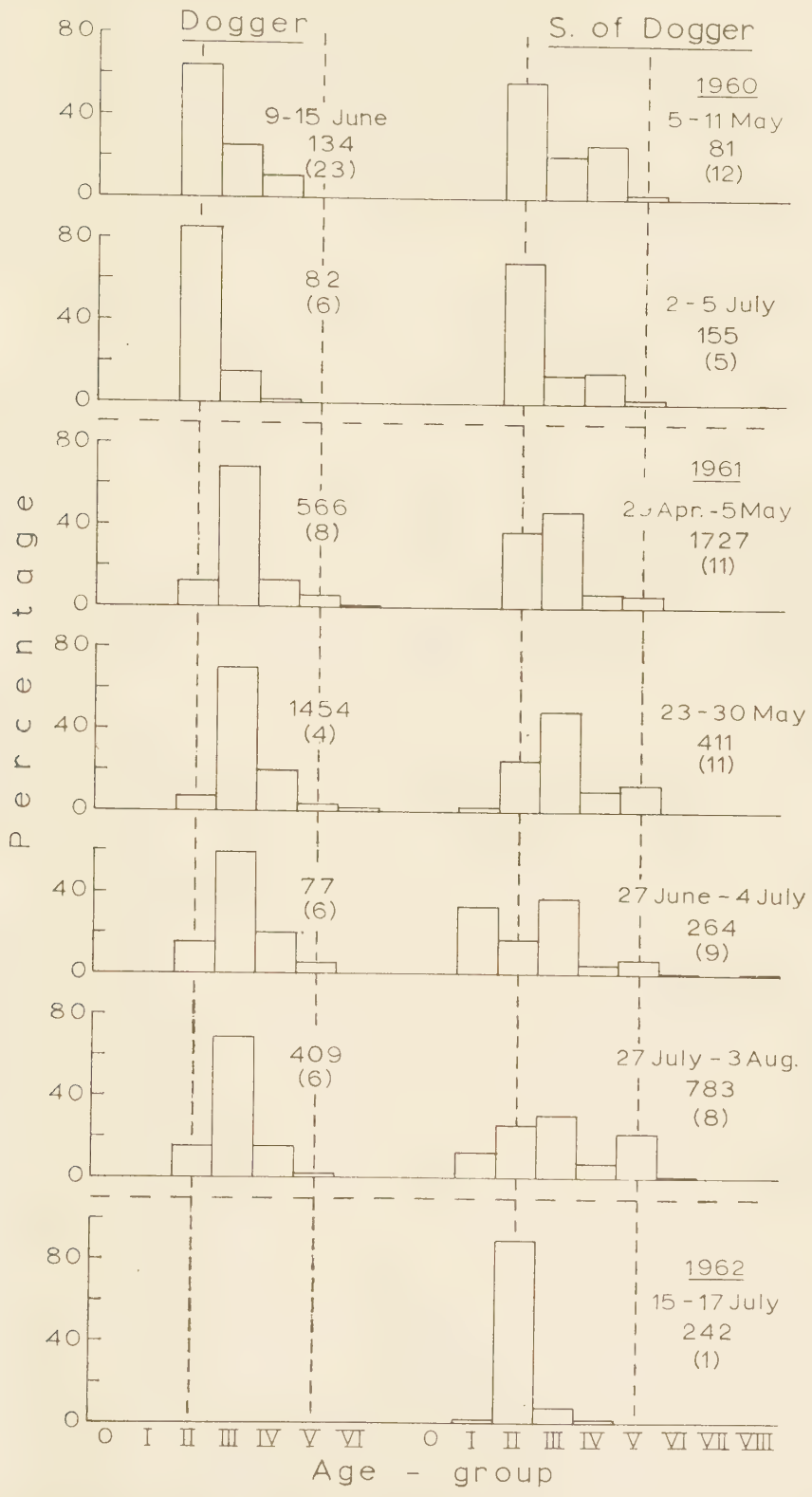


FIG. 9. *Age compositions of* A. lanceolatus *from two areas on each cruise. The numbers represent the mean numbers caught per hour and, in parentheses, the number of hauls.*

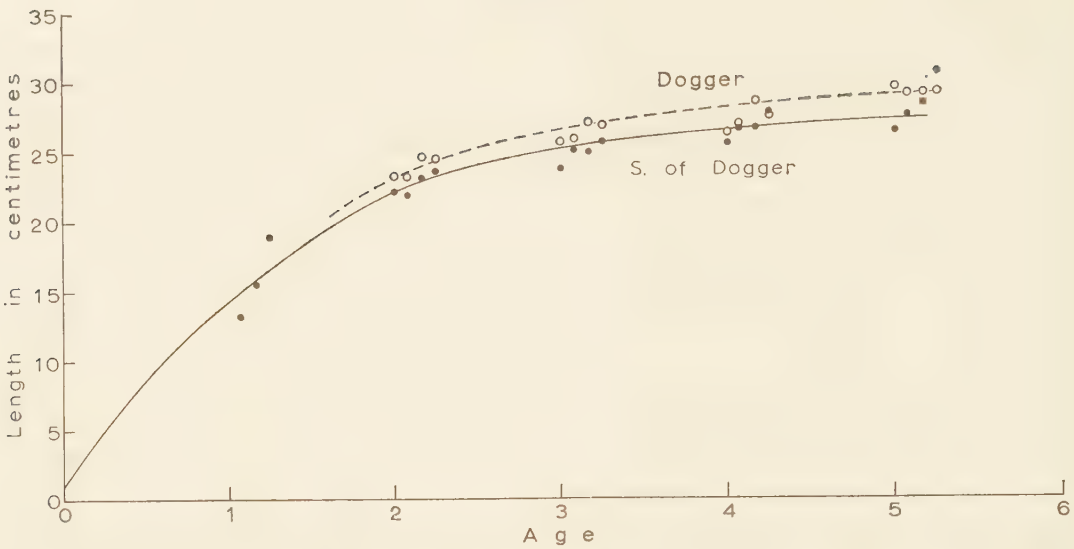


FIG. 10. *The mean lengths of different age-groups of* A. lanceolatus *at various times in* 1961 *on the Dogger and in the areas south of the Dogger.*

Table 3. A. lanceolatus. *Mean lengths of year-classes (cm), and number of fish in sample (lower figure)*

| Ground | Year-class | 1960 | | | 1961 | | | | 1962 |
|---|---|---|---|---|---|---|---|---|---|
| | | May | June | July | April–May | May–June | June–July | July–August | July |
| Dogger | 1956 | ↑ | 26·1<br>92 | 26·5<br>3 | 29·5<br>21 | 29·0<br>13 | 29·0<br>4 | 29·1<br>9 | <br>0 |
| | 1957 | | 24·8<br>210 | 25·2<br>17 | 26·3<br>45 | 26·9<br>78 | 28·5<br>14 | 27·5<br>64 | <br>0 |
| | 1958 | NS | 23·2<br>471 | 22·9<br>105 | 25·7<br>238 | 25·9<br>286 | 27·0<br>41 | 26·9<br>282 | <br>0 |
| | 1959 | | <br>0 | <br>0 | 23·3<br>43 | 23·2<br>25 | 24·6<br>10 | 24·5<br>58 | <br>0 |
| | 1960 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1961 | ↓ | – | – | 0 | 0 | 0 | 0 | 0 |
| South of Dogger | 1956 | 24·9<br>142 | ↑ | 25·5<br>32 | 26·3<br>23 | 27·5<br>38 | 28·3<br>98 | 30·5<br>95 | <br>0 |
| | 1957 | 23·7<br>118 | | 23·9<br>29 | 24·8<br>22 | 26·7<br>31 | 26·6<br>61 | 27·6<br>34 | <br>0 |
| | 1958 | 21·4<br>296 | NS | 21·2<br>224 | 23·7<br>118 | 25·1<br>142 | 24·9<br>421 | 25·7<br>189 | 30·0<br>3 |
| | 1959 | <br>0 | | <br>0 | 22·1<br>72 | 21·9<br>70 | 23·1<br>205 | 23·6<br>229 | 26·9<br>15 |
| | 1960 | <br>0 | | <br>0 | <br>0 | 13·2<br>6 | 15·5<br>177 | 18·8<br>305 | 22·1<br>181 |
| | 1961 | – | ↓ | – | 0 | 0 | 0 | 0 | 14·1<br>4 |
| Texel | 1956 | ↑ | | | | | | 0 | |
| | 1957 | | | | | | | 24·8<br>6 | |
| | 1958 | NS | NS | NS | NS | NS | NS | 22·7<br>184 | NS |
| | 1959 | | | | | | | 21·2<br>150 | |
| | 1960 | | | | | | | 19·6<br>158 | |
| | 1961 | ↓ | | | | | | 0 | |

NS = Ground not sampled.

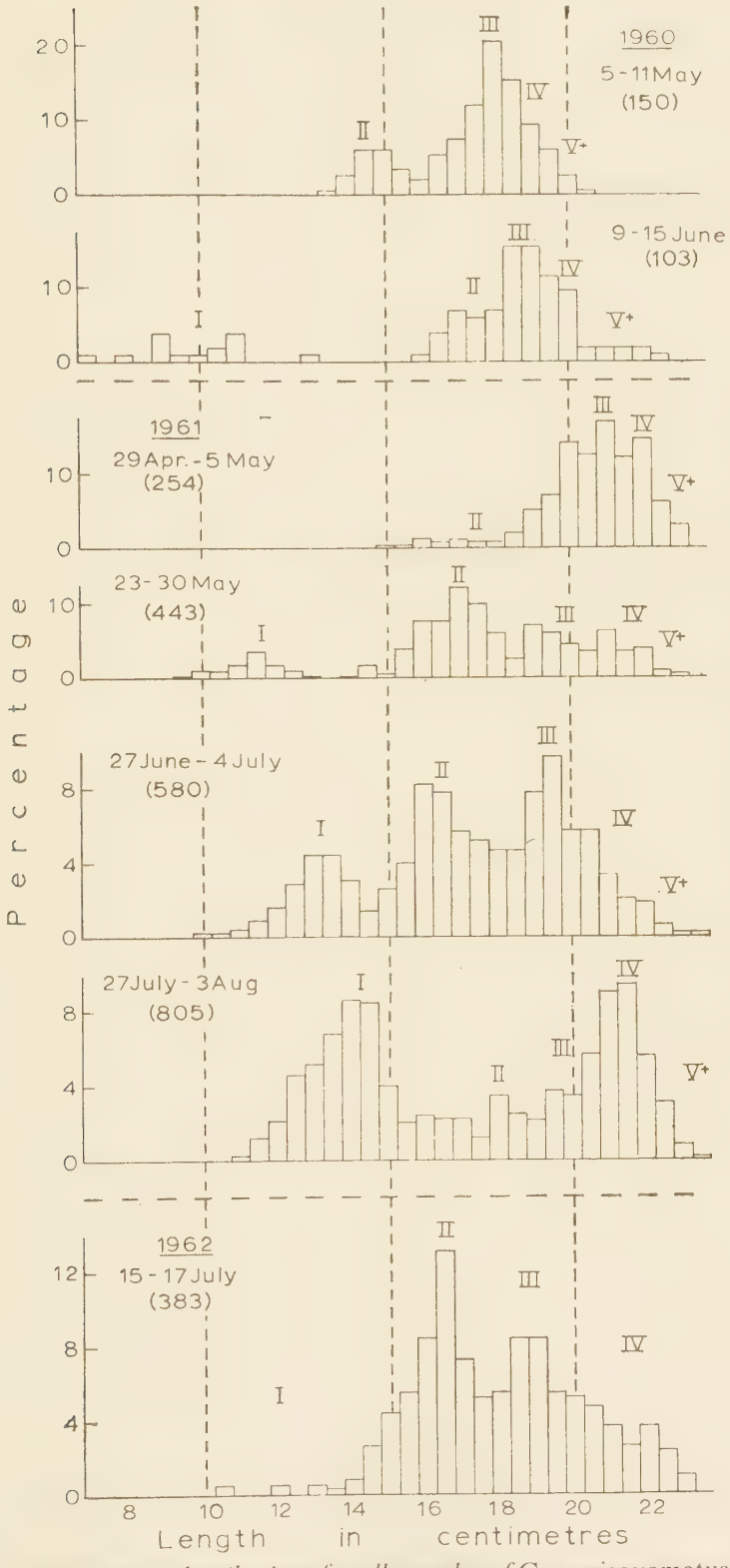


FIG. 11. *Length-frequency distributions for all samples of* G. semisquamatus *from each cruise. The numbers measured are given in parentheses and the principal age-groups are shown by Roman numerals.*

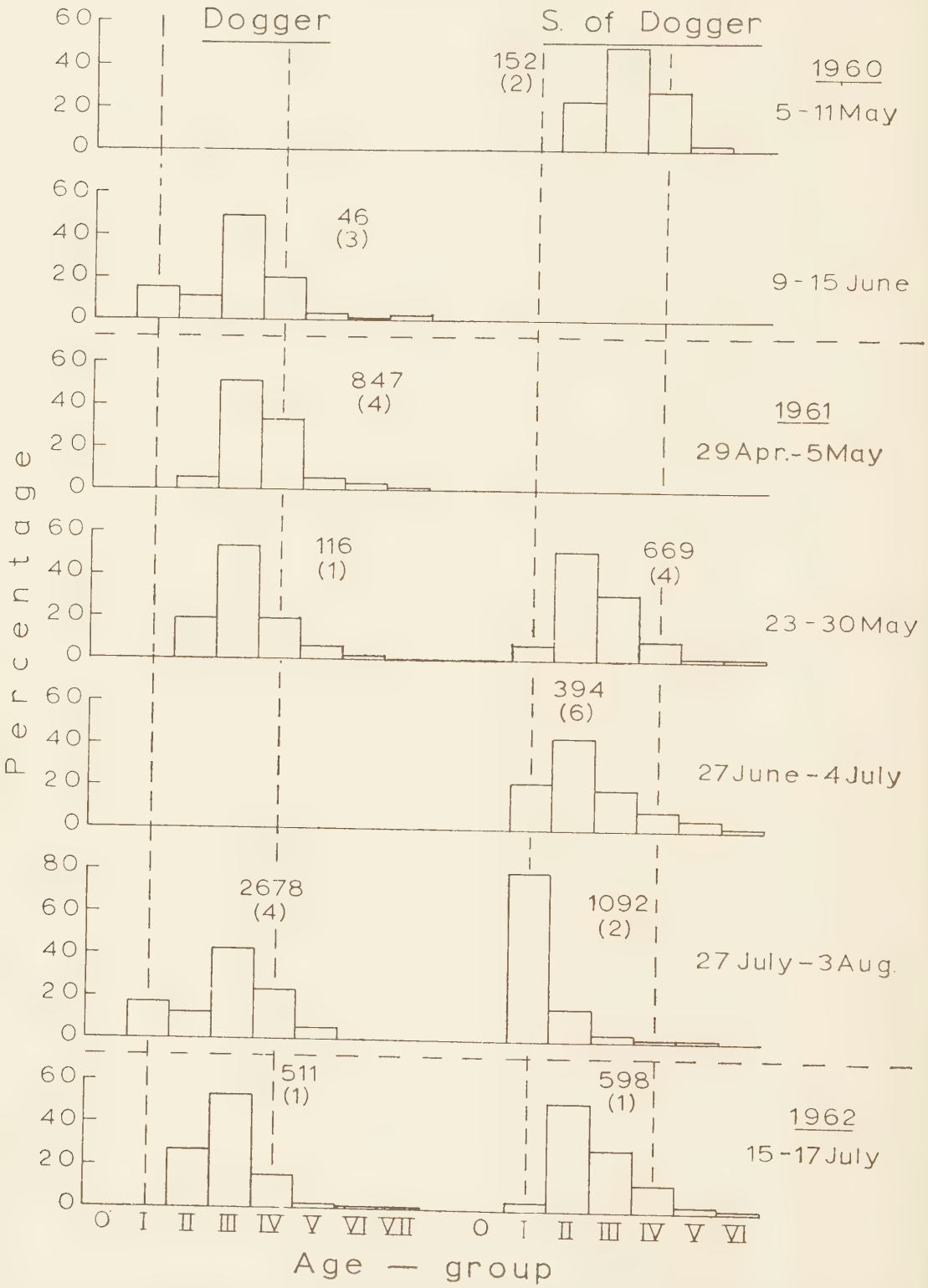


FIG. 12. *Age compositions of* G. semisquamatus *from two areas on each cruise. The numbers represent the mean numbers caught per hour and, in parentheses, the number of hauls.*

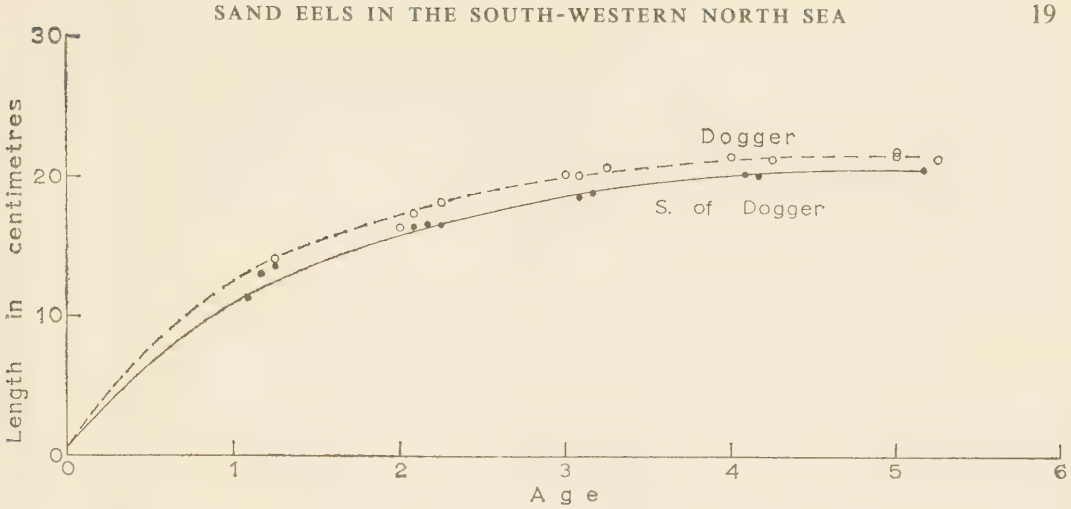


FIG. 13. *The mean lengths of different age-groups of* G. semisquamatus *at various times in* 1961 *on the Dogger and in the areas south of the Dogger.*

Table 4. G. semisquamatus. *Mean lengths of year-classes (cm) and number of fish in sample (lower figure)*

| Ground | Year-class | 1960 | | 1961 | | | | 1962 |
|---|---|---|---|---|---|---|---|---|
| | | May | June | April–May | May–June | June–July | July–August | July |
| Dogger | 1956 | ↑ | 19·6<br>23 | 21·7<br>14 | 21·8<br>7 | 0 | 21·5<br>24 | 21·5<br>3 |
| | 1957 | | 18·4<br>49 | 21·6<br>83 | 21·6<br>23 | 0 | 21·5<br>110 | 22·2<br>5 |
| | 1958 | NS | 17·6<br>9 | 20·3<br>137 | 20·2<br>62 | 0 | 20·8<br>199 | 21·4<br>39 |
| | 1959 | | 9·7<br>14 | 16·4<br>10 | 17·5<br>23 | 0 | 18·3<br>53 | 18·5<br>137 |
| | 1960 | | 0 | 0 | 0 | 0 | 14·1<br>71 | 16·0<br>71 |
| | 1961 | ↓ | – | 0 | 0 | 0 | 0 | 0 |
| South of Dogger | 1956 | 18·7<br>42 | ↑ | 0 | 19·6<br>5 | 20·7<br>44 | 19·3<br>2 | 20·6<br>2 |
| | 1957 | 17·9<br>73 | | 0 | 20·3<br>21 | 20·2<br>76 | 18·1<br>4 | 19·8<br>3 |
| | 1958 | 15·0<br>34 | NS | 0 | 18·7<br>86 | 19·0<br>126 | 18·0<br>11 | 19·5<br>19 |
| | 1959 | 0 | | 0 | 16·5<br>164 | 16·7<br>219 | 16·6<br>57 | 18·4<br>42 |
| | 1960 | 0 | | 0 | 11·3<br>47 | 13·0<br>113 | 13·6<br>276 | 16·5<br>76 |
| | 1961 | – | ↓ | 0 | 0 | 0 | 0 | 11·8<br>6 |

NS = Ground not sampled.

## GROWTH DIFFERENCES

It has been shown that sand eels on the Dogger Bank, in particular *A. marinus*, have a higher mean length than those to the south; differences could also be found within this latter area for this species. This could be accounted for either by a difference in hatching time (that is, the Dogger fish being actually older than those farther south) or by a difference in growth rate. It seems unlikely that the former is the case, since the areas are so close together.

*A. marinus*, *G. semisquamatus* and juvenile *A. lanceolatus* all feed on zooplankton and it is possible that grazing could cause local depletion of food supplies and so affect growth. Populations of sand eels from the north and south of the Outer Silver Pit are to some extent separated by this deep water channel and there is evidence for separate current regimes (Ministry of Agriculture, Fisheries and Food, 1965). Thus sand eels in these two areas could experience different densities of food. Whether this would apply in areas even closer together, such as the Haddock and Indefatigable Banks, is not so clear.

## THE WEIGHT/LENGTH RELATIONSHIP

The fish were weighed after having been deep-frozen on board ship and then thawed in the laboratory. This sometimes resulted in the rupture of the body wall, which would slightly affect the weight. Figure 14 shows the relation between weight and length in the three species; it corresponds to the usual one found in fish, i.e. $W = aL^n$ (e.g. Le Cren 1951), where W = weight in g and L = length in cm. The following values for a and n were obtained:

| | a | n |
|---|---|---|
| *A. marinus* | 0·0025 | 3·068 |
| *A. lanceolatus* | 0·0034 | 2·928 |
| *G. semisquamatus* | 0·0006 | 3·476 |

The values of n lie within the range of those found for other species (e.g. Hile 1936). Student's t-tests showed that for *A. marinus* and *G. semisquamatus* the values of n differed significantly from the cubic relation ($p \simeq 0{\cdot}02$ and 0·001 respectively), but this was not so for *A. lanceolatus* ($p \simeq 0{\cdot}12$).

## SPAWNING

### MATURITY

The state of maturity of the gonads was determined in each of the samples obtained, but the data do not cover the full maturation cycle since no samples were obtained from September to November. Various schemes for classifying the maturity stages of fish gonads have been devised (e.g. Heincke 1898, for herring; Maier 1906 (from Heincke), for plaice; Iversen 1934, for cod). The scheme used by the present author (Table 5) is a slightly modified version of that given by Cameron (1959 *a*).

In stage 2, it was found to be impossible on macroscopic examination to distinguish between a gonad re-developing after spawning and a virgin gonad developing for the first time; Bowers and Holliday (1961) found that at certain times it was impossible to separate the two stages microscopically in herring testes. In the resting gonads of sand eels it was often difficult to distinguish ovaries from testes and in these cases the gonads were examined under the lower power of a binocular microscope. Figure 15 shows the percentage of each maturity stage in the months sampled for the three species. Virgin fish (in stage 1), that is those that have not or will not spawn in that season, have not been included. Stages 3 and 4 (ripe and running respectively) have been combined, since in preserved specimens it is often difficult to decide whether the gonad was running, because the genital products tend to be coagulated by alcohol.

*A. marinus*

A sample of about 100 fish was obtained from west of Orkney on 17 November 1961 by R.V. *EXPLORER*. The age of the fish is unknown, since they had been preserved in formalin and the otoliths were unreadable. However, the modal length was 10·0 cm, which suggests that they were probably in their first year. Three of the fish were in stage 3 and the rest were in stage 1. In December 1961, twenty fish were obtained from the Channel spawning grounds in the Sandettié area. All the fish, which were I- or II-group (twenty-three months

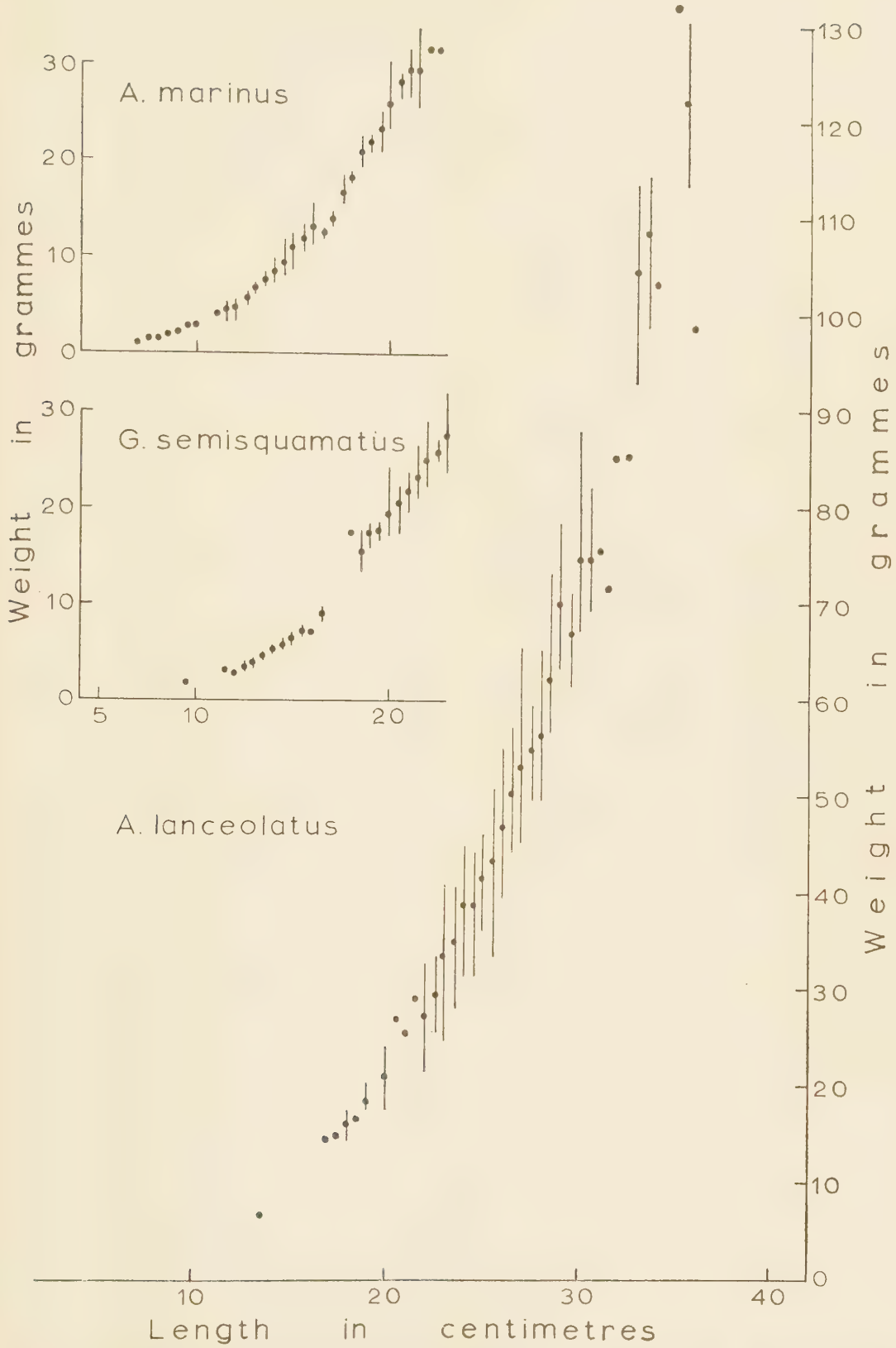


FIG. 14. *The relation between length and weight in three species of sand eels. The means and ranges of values are shown.*

Table 5. *Maturity stages in Ammodytes species (modified from Cameron, 1959 a)*

| Stage | Condition | Sex | Description |
|---|---|---|---|
| 1 | Resting or virgin | ♀ | Gonad <half body length; flattened, brownish in colour. Tunica opaque. Edges of gonad rounded; anterior end (i.e. end nearest head) slightly bilobed. No lumen. No eggs visible to naked eye. |
| | | ♂ | Gonad < half body length; flattened, greyish in colour. Edges of gonad more flattened than ovary; anterior end deeply bilobed. No lumen. Tunica opaque. |
| 2 | Developing | ♀ | Gonad from half to whole length of body cavity. Surface smooth and rounded and orange-yellow in colour. Developing eggs visible; more advanced ones on ventral side. Tunica transparent. |
| | | ♂ | Gonad from half to whole length of body cavity. Obviously bilobed. Off-white in colour but later becoming white and softer down centre. |
| 3 | Ripe | ♀ | Ovary fills cavity and is turgid. Tunica transparent and ripe eggs loose, with prominent oil globule. Blood vessels in dorsal region. Eggs cannot be expressed by slight pressure on side of fish. |
| | | ♂ | Testis fills cavity. Pure white on ventral surface but more greyish on dorsal surface. Soft, but milt cannot be expressed by gentle pressure. |
| 4 | Running | ♀♂ | As above, but gametes freely expressed by gentle pressure. |
| 5 | Spent | ♀ | Ovary a long, narrow sac. Contains dark red fluid and residual cells. Tunica loose. |
| | | ♂ | Testis flattened and empty. Contains some residual milt. Tunica loose. |
| 6 | Recovering | ♀ | Ovary shrinking. Tunica becoming thicker and opaque. Connective tissue forming in lumen. Irregular-shaped eggs being resorbed. |
| | | ♂ | Testis shrinking. Tunica becoming thicker and opaque. No residual milt; lumen being occluded. |

FIG. 15. *Seasonal changes in the state of maturity of the gonads in three sand-eel species.*

and thirty-five months respectively), were either ripe or running. A December sample was obtained from the Faroes by R.V. *ERNEST HOLT* in 1961 and all specimens were ripe or running. In early January 1962, specimens were obtained from the Dogger Bank and 50% of these were ripe or running, though a small proportion were developing. In March, the gonads were mostly recovering and resting but some were spent. From then until the end of July the gonads were recovering or resting, with the percentage of the latter increasing until it reached 100%. It is possible that the percentage of recovering (stage 6) fish has been over-estimated, since there can be difficulty in separating this stage from the resting stage 1.

This maturity cycle is broadly in agreement with Kändler's (1941) findings. He mentions three specimens taken off Heligoland on 5 December 1935 which were ripe, and also eggs of an *Ammodytes* species which were found in sand samples at this time and which probably belonged to *A. marinus*. Between April and August, all fish which he examined were 'immature'. In Manx waters, Cameron (1959 *a*) found running fish in January, February and March.

*A. lanceolatus*

Samples of this species were obtained in various years from April to August and in October and November. The most striking feature was that very few completely spent gonads were found. The majority of those assigned to stage 5 (spent) were only partially spent, whilst others assigned to stage 2 were re-developing and had already spawned previously. This was most clearly seen in the ovary, where the lumen was filled with a red fluid and degenerate ova, whilst the rest of the ovary contained healthy developing oöcytes. This indicates that *A. lanceolatus* has a prolonged spawning period, which was also Cameron's (1959 *a*) conclusion for this species in Manx waters. In the present investigation, ripe and running fish were found from April to August. The October sample came from the Moray Firth and in these fish the gonads were mostly resting but some were recovering. The November sample, in which the majority of the gonads were recovering, was from west of Orkney. Thus spawning may be slightly later here than in the Moray Firth.

*G. semisquamatus*

Samples were obtained from March to early August and ripe fish occurred in all these months. As with *A. lanceolatus*, partially spent and re-developing gonads were common, suggesting that spawning takes place over a long period. The March sample came from the Dover Strait; just over 10% were ripe, and the rest developing. The other samples were from the south-west Dogger area. Peak spawning time was in June/July, when 58% were in stage 3 or 4; by July/August, the proportion in these stages had fallen to 18·2%.

*A. immaculatus*

This species has not been included in Figure 15 since only thirty specimens have been examined from various localities. Of twenty-five fish taken in June (one from Papa Bank and twenty-four from Tory Island), two were in stage 6 and the rest were in stage 1. In July, two specimens each came from the Scilly Isles and Cape Wrath and they were all in stages 1 or 6. In November, one specimen from Broad Bay (Outer Hebrides – Lewis) was developing (stage 2). The results are in agreement with those of Corbin and Vati (1949) and Cameron (1959 *a*), who concluded that this species is a winter spawner.

## AGE AT FIRST MATURITY

In the most numerous sample of *A. marinus* obtained in the spawning period (January on the Southernmost Rough), about 5% of the one-year-old fish were ripe or recovering. Whilst the majority of the two-year-olds were mature, 19·5% were resting and presumably would not spawn till the following season; 2·1% of the older fish also showed no signs of maturing. Thus sexual maturity is normally attained when the fish is twenty-four months old, but some mature earlier at twelve months and a few perhaps at thirty-six months. Cameron (1959 *a*) finds that it is the larger fish which mature at twelve months.

*A. lanceolatus* has been found to spawn first when it is two years old, although a few

specimens have been found to be mature at one year old. *G. semisquamatus* was found to mature earlier than the previous two species, first maturity being normally attained at one year old, but it was found that up to 30% were not mature at this age. Since this species has a long spawning period (Corbin and Vati 1949, Cameron 1959 *a*, Macer 1965), it is probably the late-hatched fish which do not mature until they are two years old. Cameron (1959 *a*) finds that in Manx waters first maturity is not reached till the fish are two or three years old, and it would thus appear that they mature earlier in the North Sea.

Samples of *A. immaculatus* and *A. lancea* were insufficient to permit estimates of age at first maturity.

## SPAWNING AREAS

In the course of the investigations, much material on larval distribution was collected and the results have been published elsewhere (Macer 1965). *A. marinus* larvae were found near the Dowsing and Southernmost Rough (Dogger) areas, and also in the Southern Bight; larvae of *A. lanceolatus* and *G. semisquamatus* occurred in similar areas. Further evidence on spawning areas is provided by maturity data, and Figure 16 shows the positions in the

FIG. 16. *Localities where ripe adults were taken.* ×A. marinus; ●A. lanceolatus; ○G. semisquamatus.

Dogger and South of Dogger areas where ripe adults of the three species were caught. For *A. marinus* this was on the Southernmost Rough ground; both *A. lanceolatus* and *G. semisquamatus* were, however, taken over a wide area of the south-west Dogger and Norfolk Banks. *G. semisquamatus* was also taken in the Dover Strait area (Bassurelle Bank and Varne L. V.), *A. lanceolatus* in the Texel area, and *A. marinus* in the Sandettié area.

## SEX RATIO

As in previous sections, fish from the Dogger and South of Dogger areas were treated separately and the proportions of each sex determined.

*A. marinus*

Most of the samples were obtained in the months from March to August, during which time the gonads were recovering and later resting. In both areas, during this period, the sex ratio remained fairly constant, with a preponderance of females in all cruises except one, where there were equal numbers of males and females. There was no significant difference between the sex ratios in the two areas; the overall sex ratio was 45·0% males and 55·0% females (2 252 fish). This is significantly different from a 50/50 ratio ($\chi^2$ test, $p < 0{\cdot}001$).

On two cruises – on the Dogger in early January and in the Southern Bight in mid-December – spawning fish were taken, and at these times the sex ratio was reversed. On the first cruise, males comprised 66·7% (120 fish) and on the second, 65·0% (20 fish). This reversal applied to the immature as well as the mature fish, though it was more marked in the latter.

*A. lanceolatus*

All the samples of this species were obtained during the spawning season. Although there was much variation between monthly samples, taken together the sexes occurred in equal numbers on grounds to the south of the Dogger (51·0% males, 49·0% females, 1 126 fish) but on the Dogger itself there was a preponderance of females (54·8%, 597 fish). This ratio differs significantly from that in the other area ($\chi^2$ test, p between 0·05 and 0·02). There was no difference in sex ratio between mature and immature fish.

*G. semisquamatus*

As with *A. marinus*, there was no difference between the ratio in the two areas. There were variations from month to month, but the total ratio did not differ significantly from 50/50 (49·0% males and 51·0% females, 626 fish). In June, July and August there seemed to be a trend towards an increase in the proportion of males. All samples were taken in the spawning season.

The high male: female ratio in *A. marinus* in its spawning season is of interest, since this also occurs in plaice (Hefford 1909, 1916, Simpson 1959). The reason for the phenomenon could be either that there is a difference in behaviour between the sexes at spawning time or that more males are in fact present, which implies some sort of spawning migration. For plaice, Hefford (1916) concluded that the unequal sex ratio was probably due to the males remaining longer on the spawning grounds than the females. However, there is evidence that male plaice are more susceptible than females to capture by a trawl throughout the year (Beverton 1964).

## FECUNDITY

For estimates of fecundity, only those ovaries which are ripe but have not shed any ova should be used. In the case of *A. marinus*, which has a short spawning period and sheds its eggs fairly quickly, it is fairly obvious which ovaries can be used. However, both *A. lanceolatus* and *G. semisquamatus* shed their eggs over a long period and, although estimates were made for these two species, they varied so widely that it was clear that many of the ovaries used were partially spent, and the results have therefore not been included.

The ovaries were initially preserved in 90% alcohol but later transferred to a modified Gilson's fluid (see Simpson 1951). The eggs were then separated by passing them through

appropriately-sized sieves with the aid of a fine jet of water, and this was repeated several times so that nearly all the ovarian tissue became separated from the eggs. They were counted electronically in an apparatus using a photo-electric cell, developed by my colleague, R. B. Mitson. In trials where known numbers of eggs were passed through the apparatus it was found to be 100% accurate. However, in the samples the eggs could never be completely cleared of pieces of ovarian tissue, and the counts are likely to be slight overestimates, since these pieces would be counted.

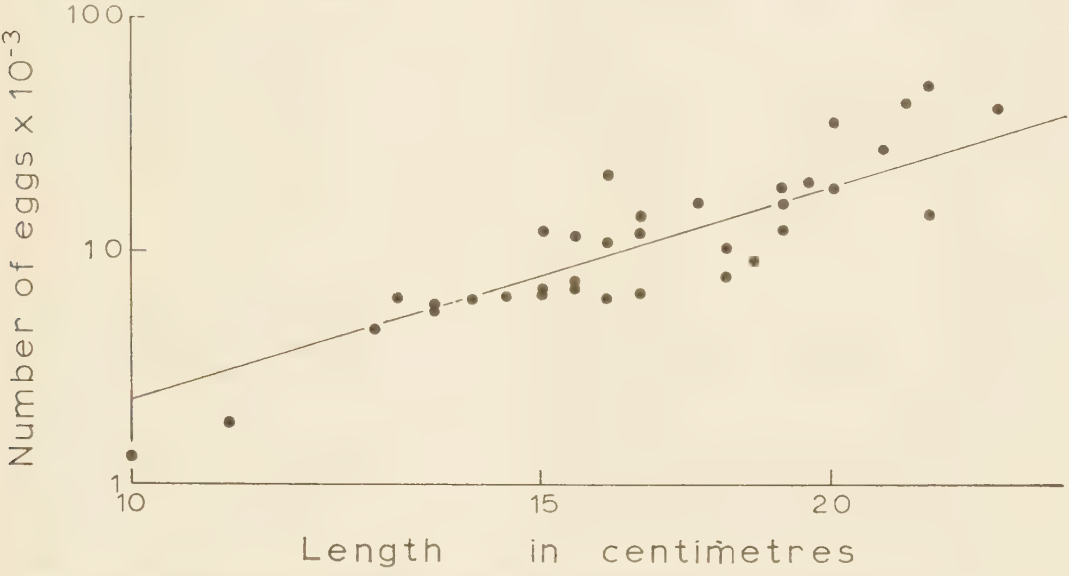


FIG. 17. *The relation between the logarithms of fecundity and length of fish in* A. marinus.

In Figure 17 each estimate of the number of eggs found in *A. marinus* is plotted against length. The fish were taken at Faroe in December 1961 and from the Southernmost Rough in early January 1962. The regression of fecundity on length gives the following relation:

$$\text{Fecundity} = 2{\cdot}046 \times \text{length}^{3{\cdot}055}$$

As can be seen from Figure 17 there are wide variations in the number of eggs per length group and this has been noted in other species (Fulton 1891, Simpson 1951, Hodder 1963). The fact that fecundity is proportional to a power of the length is also in agreement with previous findings for other species (Raitt 1933, Hickling 1940, Simpson 1951, Hodder 1963), and in most cases fecundity increases as the cube, or more, of the length. For *A. lancea*, Fulton (1891) gives fecundities for two fish of 14 and 18 cm as 13 350 and 36 305 respectively (these are larger than the present values for *A. marinus*); for *A. lanceolatus* he gives three values, the eggs being divided into large and small. They are as follows:

| Length (cm) | Number of Ova | | |
|---|---|---|---|
| | Small | Large | Total |
| 30·6 | 28 826 | 33 242 | 62 068 |
| 30·6 | 28 166 | 33 583 | 61 749 |
| 24·2 | 19 947 | 17 580 | 37 527 |

Values for *A. marinus* of corresponding lengths, 30·6 and 24·2 cm, obtained from Figure 17 by extrapolation, are 102 118 and 43 152, and thus the fecundity is higher than in *A. lanceolatus*.

Further data on the duration of spawning may be obtained from measurements of the eggs (Hickling and Rutenberg 1936), and such measurements for the three sand-eel species

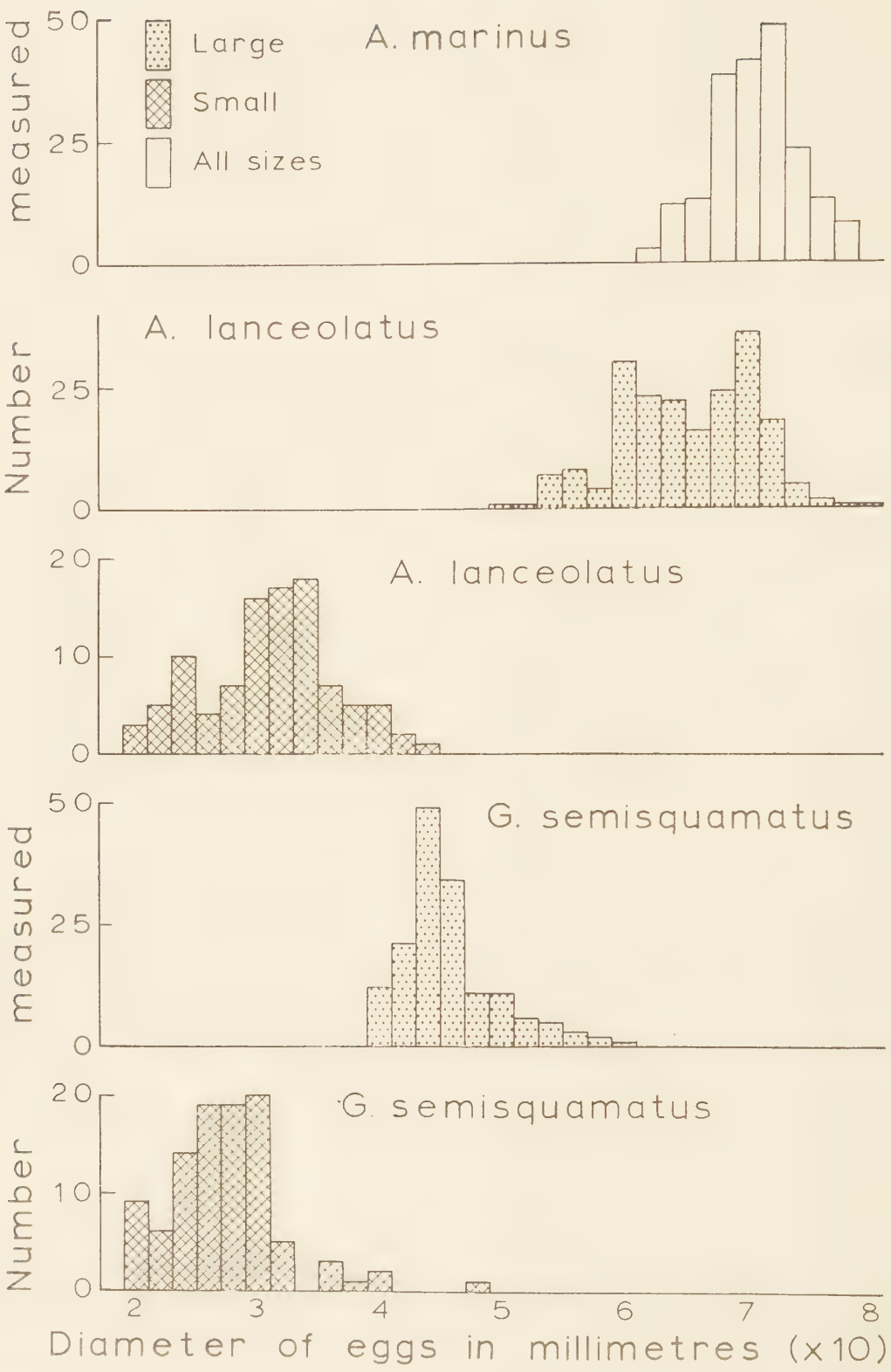


FIG. 18. *Frequency distribution of egg-diameter measurements in three sand-eel species.*

are shown in Figure 18. The eggs were measured after a long period of preservation and had almost certainly shrunk. McIntosh (1891) gives the average size of fresh *A. lanceolatus* eggs as 0·7620 mm, which is somewhat larger than that found in the present work. With *G. semisquamatus* and *A. lanceolatus*, two sizes of eggs separated out during the sieving process previously mentioned and these have been shown separately in Figure 18, because some of the larger eggs had probably been shed and hence the true proportion of large to small is unknown. As shown above, Fulton (1891) also described two size groups of eggs for *A. lanceolatus* and found no great differences in the numbers of small and large eggs. In *A. marinus* the eggs have a unimodal size distribution but in the other two species it is bimodal, indicating at least two batches of eggs. Thus the egg measurements agree with data on seasonal occurrence of larvae (e.g. Macer 1965) and maturity stages, which show that *A. marinus* has a short spawning period and *A. lanceolatus* and *G. semisquamatus* prolonged ones.

## FEEDING

The numbers of stomachs of each species examined in various months are set out in Table 6 and the results of the stomach analyses are shown in Table 7. Since samples were inadequate to show any seasonal changes in diet, all the monthly samples have been combined. Each sand-eel species has been divided into size groups and the food organisms recorded by the 'occurrence' method (e.g. Hynes 1950). The numbers against each food item in Table 7 represent the proportion (as mean percentage weighted by the number of stomachs examined in each month) of stomachs containing food in which that particular food item occurred. In addition, the fullness of each stomach (as a rough percentage) was noted, as was the dominant food organism with respect to volume of organic matter (estimated by eye), though the latter is not recorded in the table. *A. immaculatus* has not been included in Table 7, since few stomachs were obtained.

Table 6. *Numbers of sand-eel stomachs examined*

| | J | F | M | A | M | J | J | A | S | O | N | D | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *A. marinus* | 20 | | 25 | | 130 | 80 | 25 | | | | 1 | 15 | 296 |
| *A. lanceolatus* | 5 | | 10 | | 97 | 84 | 36 | | | 10 | | | 242 |
| *G. semisquamatus* | | | 5 | | 15 | 31 | | | | 10 | | 2 | 63 |
| *A. lancea* | | | | | 1 | 30 | 13 | | | | | 2 | 46 |
| *A. immaculatus* | | | | | | 1 | 3 | | | | 1 | | 5 |

*A. marinus*

The chief food organisms are copepods, crustacean larvae and annelids. In the smallest size group (< 10 cm) copepods – chiefly *Calanus* and *Temora* – are the most important item and often the stomachs are packed with them, *Temora* predominating. The invertebrate eggs are probably of copepods also. As the fish grow larger, annelids, mainly newly metamorphosed polychaetes, become more important and *Calanus* is taken more frequently than *Temora*. In general, there is a tendency for the larger fish to take bigger food items, and in addition to these examples of copepods and annelids, the larger crustacean larvae (the zoea and megalopa stages) occur more frequently than the smaller ones (cyprids).

*A. lancea*

Copepods are the dominant food, with *Temora* most important. The five fish examined in the 16 20 cm group, however, contained fish scales and annelids, the latter also being important in the smaller fish. It is interesting to note that crustacean larvae did not occur, whilst amphipods, mysids and Cladocera were found more frequently than in *A. marinus*. The variation in stomach contents between this species and *A. marinus* probably reflects the difference in habitat – inshore and offshore.

Table 7. *Proportion of sand-eel stomachs, containing food, in which each food item occurred (weighted mean %)*

| Species | *A. marinus* | | | *A. lancea* | | | *G. semisquamatus* | | | *A. lanceolatus* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Length (cm) | <10 | 10–20 | >20 | <10 | 10–15 | 16–20 | <10 | 10–20 | >20 | <15 | 15–25 | >25 |
| No. of stomachs | 59 | 207 | 30 | 20 | 21 | 5 | 5 | 47 | 11 | 19 | 162 | 61 |
| Number empty | 7 | 40 | 17 | 0 | 3 | 0 | 0 | 6 | 4 | 6 | 45 | 20 |
| Range of fullness % | 0–100 | 0–100 | 0–100 | 20–100 | 0–100 | 50–60 | 50–80 | 0–100 | 0–30 | 0–100 | 0–100 | 0–100 |
| Mean % fullness | 69 | 50 | 17 | 91 | 49 | 54 | 66 | 34 | 11 | 58 | 45 | 44 |
| Sand grains | 15·3 | 9·6 | 8·0 | 30·0 | 27·5 | 0 | 0 | 19·5 | 28·3 | 15·4 | 0·9 | 0 |
| Fish scales | 0 | 0 | 0 | 0 | 50·0 | 80·0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Fish adults | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 36·7 | 56·2 |
| Fish larvae | 1·9 | 3·1 | 8·0 | 0 | 0 | 0 | 0 | 0 | 14·6 | 30·8 | 30·9 | 22·3 |
| Fish ova | 9·6 | 14·8 | 15·0 | 0 | 0 | 0 | 0 | 2·4 | 14·6 | 30·8 | 13·0 | 2·4 |
| Invertebrate ova | 36·3 | 30·2 | 8·0 | 35·0 | 0 | 0 | 100·0 | 31·6 | 28·3 | 0 | 0 | 0 |
| Copepods | 96·6 | 84·7 | 54·0 | 100·0 | 50·0 | 0 | 100·0 | 92·7 | 71·1 | 46·2 | 25·2 | 17·0 |
| Calanus | 30·9 | 22·8 | 30·0 | 5·0 | 0 | 0 | 20·0 | 41·4 | 14·6 | 0 | 3·7 | 9·7 |
| Temora | 69·4 | 64·1 | 23·0 | 60·0 | 33·0 | 0 | 100·0 | 58·5 | 14·6 | 26·7 | 12·2 | 2·4 |
| Centropages | 5·9 | 5·6 | 0 | 15·0 | 0 | 0 | 20·0 | 0 | 0 | 0 | 0 | 0 |
| Pseudocalanus | 17·5 | 27·4 | 15·0 | 15·0 | 5·8 | 0 | 100·0 | 41·5 | 28·3 | 0 | 1·9 | 0 |
| Acartia | 0 | 0·5 | 0 | 50·0 | 0 | 0 | 40·0 | 0 | 0 | 0 | 0 | 0 |
| Anomalocera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2·4 | 0 | 0 | 5·0 | 0 |
| Paracalanus | 0 | 0 | 0 | 0 | 0 | 0 | 20·0 | 0 | 0 | 0 | 0 | 0 |
| Caligus | 0 | 0 | 0 | 15·0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Crustacean larvae | 23·2 | 43·9 | 15·0 | 0 | 0 | 0 | 20·0 | 22·0 | 28·3 | 23·1 | 21·5 | 21·8 |
| Cyprid | 23·2 | 30·8 | 0 | 0 | 0 | 0 | 0 | 14·6 | 0 | 0 | 2·6 | 0 |
| Zoea and Megalopa | 2·0 | 23·8 | 15·0 | 0 | 0 | 0 | 20·0 | 17·0 | 28·3 | 23·1 | 18·9 | 21·8 |
| Amphipods | 11·6 | 2·3 | 23·0 | 35·0 | 5·8 | 0 | 0 | 9·8 | 14·6 | 0 | 1·3 | 0 |
| Mysids | 1·9 | 0 | 0 | 15·0 | 5·8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Euphausids | 1·9 | 3·0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23·1 | 10·3 | 12·1 |
| Isopods | 2·0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cumacea | 1·9 | 0 | 8·0 | 0 | 0 | 0 | 0 | 9·8 | 0 | 0 | 0 | 0 |
| Cladocera | 0 | 2·6 | 0 | 10·0 | 0 | 0 | 0 | 4·9 | 0 | 0 | 0 | 0 |
| Chaetognatha | 9·7 | 5·5 | 15·0 | 0 | 0 | 0 | 0 | 9·8 | 14·6 | 0 | 0 | 0 |
| Larvacea | 3·9 | 11·8 | 15·0 | 0 | 0 | 0 | 40·0 | 17·0 | 28·3 | 0 | 1·7 | 0 |
| Molluscs | 3·8 | 0·5 | 0 | 0 | 0 | 0 | 0 | 4·9 | 0 | 0 | 0 | 0 |
| Annelids | 27·1 | 45·7 | 70·0 | 30·0 | 44·2 | 20·0 | 100·0 | 46·3 | 42·9 | 0 | 4·8 | 2·7 |
| Echinoderms | 0 | 0·6 | 0 | 0 | 0 | 0 | 0 | 2·5 | 0 | 0 | 0 | 0 |
| Coscinodiscus | 11·8 | 4·7 | 0 | 0 | 0 | 0 | 20·0 | 0 | 0 | 0 | 0 | 0 |
| Miscellaneous | 0 | 1·1 | 8·0 | 15·0 | 5·8 | 0 | 0 | 0 | 0 | 0 | 0·9 | 0 |

*G. semisquamatus*
Once again copepods and annelids are the two most important food items. A greater variety of copepods is taken by this species than by *A. marinus* or *A. lancea*. Decapod larvae (which are important in that they are larger than most copepods) and Larvacea occur quite frequently.

*A. lanceolatus*
Fish, in the form of eggs, larvae, or adults, constitute the main food of this species except for the smallest individuals. Those less than 15 cm in length take fish larvae and eggs, copepods, crustacean larvae and euphausids. With increasing size, adult fish become the most important item, the most common prey being *Ammodytes* itself, though not its own species.

*A. immaculatus*
Fish have been found in the few stomachs of this species which have been obtained.

Although this study has been by no means exhaustive, the samples being taken chiefly in May, June and July, it is sufficient to show the main types of food taken. *A. marinus*, *A. lancea* and *G. semisquamatus* are clearly plankton feeders, taking mainly copepods and juvenile annelids. This is in agreement with Roessingh's (1957) conclusion. In marked contrast to this, *A. lanceolatus* (and probably *A. immaculatus*) are predators on other fish, chiefly sand eels, although the smaller ones tend also to take planktonic food. It is well known that *A. lanceolatus* can be taken on artificial lures (such as when 'jigging' for mackerel), which tends to indicate a predatory nature.

It is perhaps surprising to find plankton-feeding in fish which are adapted to live in close association with the bottom, though it is probable that they feed just above the bottom. It is not known if there are diurnal changes in feeding, since no sand eels were caught at night, but around the coast of Hokkaido, Motoda and Tanaka (1950) found that feeding ceased at night in *A. personatus*. As in the present investigation, the chief food item was copepods.

# PART II – THE FISHERY

## DEVELOPMENT

The first large-scale landings of sand eels were made in 1953 at Esbjerg in Denmark, the quantity being about 4 500 tons (Popp Madsen 1957). Small amounts had been landed at fish-meal factories before this, however, for example in 1952 in Germany (Meyer-Waarden 1959), but it was not until 1955 that the latter country landed large quantities (figure not recorded), to be closely followed by Norway in 1956 and the Netherlands in 1957.

The reason for the start of the fishery, which is purely industrial, seems to have varied with each country. The principal consideration appears to have been that it provided the fish-meal factories with supplies of fish in what would have been a slack period between the winter and late summer industrial fisheries for herring (Anon. 1957 *b*). In the case of the Dutch fishermen, it was evidently a poor season for soles that prompted them to start fishing for sand eels (Roessingh 1957).

The fishery is a seasonal one and normally lasts from April to July, exceptionally from March to August. The boats used vary according to the country but are mostly wooden vessels of the seiner/cutter type, and such vessels form the bulk of the Danish sand-eel fleet of about 400 boats. They are mostly about 60–70 feet in length and have a capacity of 40–70 tons. The Dutch fleet formerly comprised about 45 cutters, of about 75 feet, with engines of between 150–240 hp, but in later years some smaller cutters (about 120 hp) have fished in pairs for sand eels (Roessingh, personal communication). In Germany, up to 169 cutters have fished for sand eels (Kühl 1957). Little information is available on the Norwegian vessels, but about 10 trawlers and a factory ship have been recorded (Anon. 1957 *b*).

The gear varies only slightly and is a cotton and nylon Vinge trawl with a light footrope and high headline; bridles up to 35 fathoms long are used and the cod-end mesh is 6 mm bar.

In the first instance, the boats fished close to their own coasts. The Danish boats concentrated on the Horns Reef area, the Germans on Terschelling and Borkum Rough, and the Dutch from Texel to the Zeeland Isles. In 1956, the Danes found concentrations of sand eels to the north and south of the Outer Silver Pit and have since fished there in the early part of the season. The Germans did likewise in 1960 and the Norwegians now fish there also. The Dutch boats appear to have remained in their own coastal areas. There is a small fishery in the Skagerrak and Kattegat (Region IIIA) by Denmark and Norway.

The principal fishing grounds are shown in Figure 19, on which is also indicated the 20-fathom contour. It can be seen that the fisheries occur in depths of less than 20 fathoms where the bottom is sandy.

On the eastern side of the North Sea the fishing grounds extend from the Jutland Bank, off the Danish coast, along the coastal areas of Denmark, Germany and Holland to the Zeeland Isles. On the western side of the North Sea, they occur around the south-western edge of the Dogger Bank (Southernmost Rough, South-West Spit, and Outer Well Bank), and between the southern edge of the Outer Silver Pit and the Norfolk coast, mainly on the Norfolk Banks (e.g. Indefatigable, Swarte and Haddock Banks) but also off the Banks (e.g. Well Bank Flat, and around Sole Pit and Well Hole).

## LANDINGS

Accurate statistics of the sand-eel fishery are very difficult to obtain. Up to and including 1960, landings were included with other fish under the heading 'various' in the international

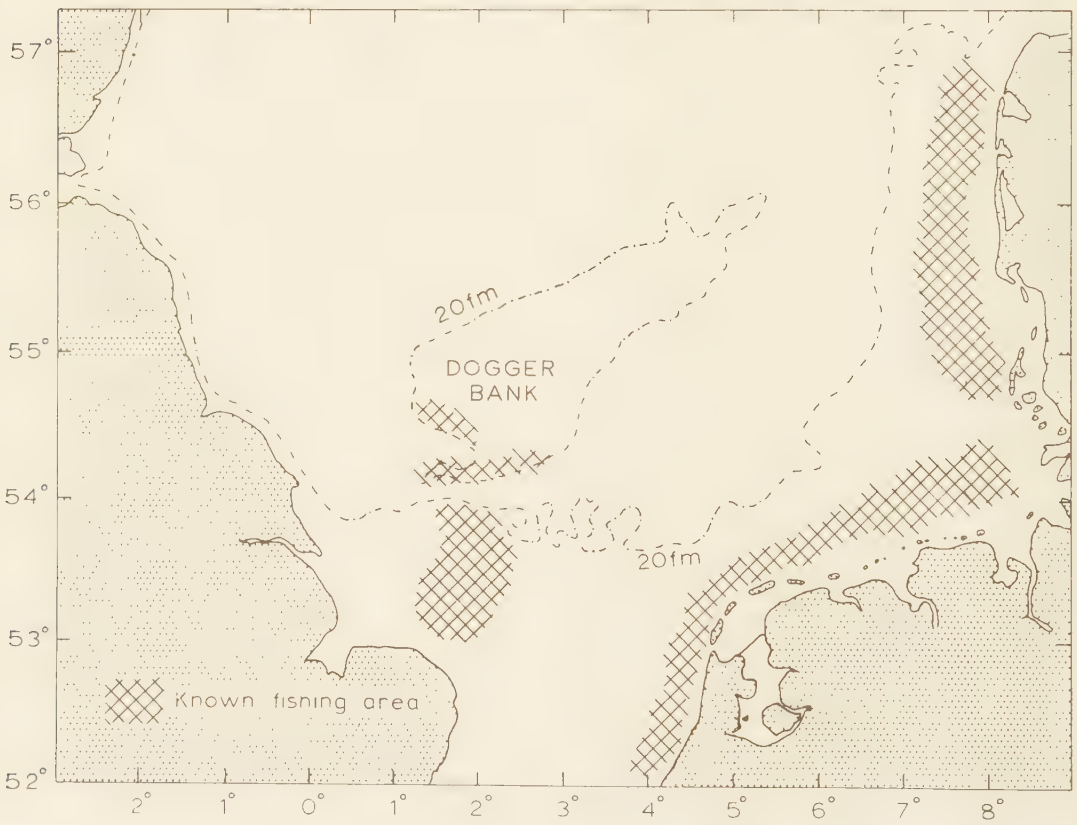


FIG. 19. *Areas in the North Sea where sand-eel fisheries are known to have taken place.*

statistical publication 'Bulletin Statistique des Pêches Maritimes', and were recorded separately only by Holland and Norway in some years. Elsewhere, figures for total landings tend to vary, so that the data given here may differ from other published data. The source of the present figures is stated for each country. Figure 20 and Table 8 show the annual landings of sand eels for each country and also the total landings. The latter increased rapidly up to 1956 but then remained fairly constant at about 100 000 tons per annum. There was a fairly sharp rise in 1960 due to increased landings by Norway and Denmark, and after a decline in 1961, total landings increased markedly in 1962 and 1963. By far the greatest quantities are landed by Denmark and it can be seen that the total landings closely reflect those of this country; in 1963, for example, her total of 155 900 represented 84·8% of all landings. German landings increased rapidly in 1957 but then declined; in 1963, however, there was a marked increase. Norwegian catches built up more slowly to a peak of 13 688 metric tons in 1960 and have since remained fairly steady. The Netherlands catch fluctuated from 1957 to 1959 but their fishery virtually ceased in 1960.

In recent years, some small landings of sand eels have been made at Hull and Grimsby by Danish vessels, and in 1964 there were some small English landings.

Data on effort are available for Germany for each year from 1956 (Lundbeck 1956 et seq.), and Bertelsen and Popp Madsen (1958) have published catch per unit of time for a Danish fishery in 1958. The German data are plotted in Figure 21; the catch per trip shows a slight but steady decline until 1960 when it increases sharply. This increase is probably due to the fact that, until 1959, the German fleet was fishing near its own coastline but in 1960 it started to fish the south-west Dogger area (Meyer-Waarden 1962). Catch per trip showed a further rise in 1961, despite a steady decrease in total landings and in effort, but then a fall in 1962.

## MONTHLY VARIATION IN CATCH

Figures for monthly landings show a peak in June and this peak also occurs in the commercial catch per effort data, as shown in Figure 22 for Germany (from Lundbeck 1956 et seq.) and Denmark (from Bertelsen and Popp Madsen 1958). Also shown in Figure 22 is the average number of sand eels caught per hour by R.V. *PLATESSA* from 1960–1962 (only known commercial grounds have been included). In the case of *PLATESSA's* hauls the maximum numbers occurred in January, at a time when there is no commercial fishery. The increase in catch per effort by the commercial boats in the early part of the year may be explained to some extent by an increase in fishing efficiency; because shoals of sand eels are very localized, as more vessels join the fleet its searching power and fishing efficiency will improve. However, it seems unlikely that this could account for all of the increase. Part of it may be due to recruitment to the fishing areas and to mesh selection. Two samples of *A. marinus* which were taken from the cod-end meshes in January 1962 and March 1960 had modal lengths of 9·0 and 8·0 cm respectively; the selection length must thus be a little smaller than these lengths. By considering the monthly length distributions of this species (Figure 3) it is seen that some I-group fish could escape through the meshes in the early part of the year, especially in the case of the relatively slow-growing fish south of the Dogger. In addition, some O-group fish reach the selection length in May/June on the Dogger Bank and in July/August on some of the grounds to the south.

The seasonal increase in density of fish could also be explained if recruitment to the fishing areas took place over a long period. It is known that some recruitment can occur as soon as the larvae leave the plankton, since newly metamorphosed *A. marinus* (3–4 cm in length) have been found in the stomachs of *A. lanceolatus* adults on the fishing grounds from late April onwards. However, if the larvae were carried for long distances in surface currents due to strong winds and the juveniles then made their way back against the current, as might happen (Macer 1965), this would prolong recruitment. There is some evidence for the latter, from mortality data (Figure 25 – see below).

It is doubtful whether the above phenomena could account completely for seasonal density increases of the magnitude shown in Figure 22. In the *PLATESSA* data, for example, there

FIG. 20. *Total landings in sand-eel fisheries by each country; landings include by-catch, except for Germany.*

Table 8. *Landings of sand eels from the North Sea (Region IV) by each country (in metric tons)*

| | 1953 | 1954 | 1955 | 1956 | 1957 | 1958 | 1959 | 1960 | 1961 | 1962 | 1963 | Source of data |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Denmark* | 4 500[1] | 11 000[1] | 42 000[2] | 88 000[2] | 76 000[2] | 74 600 | 78 000 | 105 000 | 78 200 | 127 000 | 155 900 | *Liaison Committee Report (ICES)* |
| Germany | ? | ? | ? | 5 298 | 25 524 | 22 000 | 21 248 | 7 884 | 4 235 | 968 | 16 400[4] | Lundbeck[3] |
| Norway* | – | – | – | 1 435 | 3 220 | 4 817 | 7 979 | 13 688 | 5 400 | 11 602 | 11 563 | *Statisk Arbok for Norge* |
| Netherlands | – | – | – | – | 3 700[2] | 1 522 | 5 062 | 3 | 64 | – | – | *Bulletin Statistique* |
| Total | 4 500+ | 11 000+ | 42 000+ | 94 733 | 108 444 | 102 939 | 112 289 | 126 575 | 87 899 | 139 570 | 183 863 | |

* Small amount landed from Region IIIA.
[1] Popp Madsen (1957).
[2] Anon. (1960 *b*).
[3] Figures exclude by-catch.
[4] Liaison Committee Report (ICES).

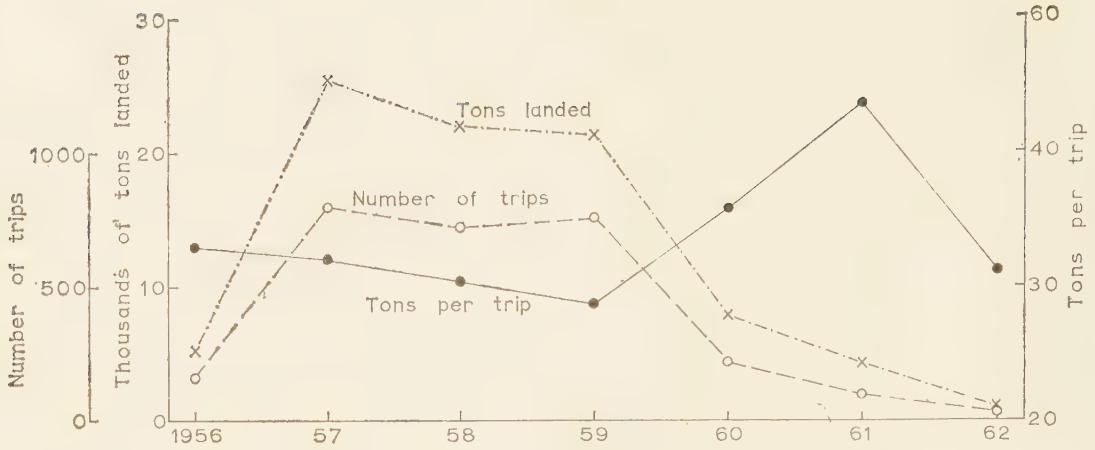


FIG. 21. *German sand-eel statistics (from Lundbeck 1958 et seq.).*

was no widespread increase in catch per unit effort of I-group *A. marinus* as the season progressed. Seasonal changes in catch per unit effort are unlikely to be caused to any great extent by variations in density of *A. lanceolatus* or *G. semisquamatus*, since these species form such a small part of the sand-eel stocks.

It was thought that behavioural differences might explain the seasonal density changes, since there is evidence that sand eels bury themselves in the sand in winter (Cameron 1959 *a*). Early work by *PLATESSA* seemed to support this hypothesis, in that few or no sand eels were caught in the sand-eel trawl in winter. However, none were taken in various bottom samplers such as dredges and grabs, so winter availability of sand eels remained something of a mystery. In early January 1962, however, a very large number (305 000 fish) of *A. marinus* were caught in a one-hour tow on the Southernmost Rough; over 99% were I-group immature fish. Out of five hauls on this ground two were completely blank and only three fish were taken in four hauls in the Dowsing area. In all winter cruises very few sand eels of species other than *A. marinus* have been caught.

The results of the winter sampling suggest that, at least for the immature fish, the shoals are then more compact than in summer. Since very few mature specimens of *A. marinus* were caught, it is possible that this applies to them too but they may be less 'catchable' also, due to spawning behaviour. There was no evidence from the present work that this species lives buried in the sand in winter. The decline in catch per effort by commercial vessels after June is probably due to reduction in stock size, mainly as a result of fishing.

## DIURNAL VARIATION IN CATCH

The sand-eel fishery is carried out in daylight only, since very few sand eels are caught at night (Bertelsen and Popp Madsen 1958; Roessingh 1957). Figure 23 shows three twenty-four hour stations, two of them (A and B) worked by the Danish research vessel *DANA* (data from Bertelsen and Popp Madsen) and the third (C) by R.V. *PLATESSA*. The stations shown in B and C were on the Southernmost Rough, and that in A a few miles away. On all three stations few or no sand eels were caught during the hours of darkness; catches rose during daylight hours, though the time of maximum catch varied. In addition to the twenty-four hour station worked by *PLATESSA*, regular hauls were made during daylight on the Southernmost Rough on three cruises, and the results of these are shown in Figure 24 for the three species. Each set of three histograms represents hauls on the same day. Much variation occurred in the maximum numbers caught during the day, both between different species on the same day and between the same species on different days.

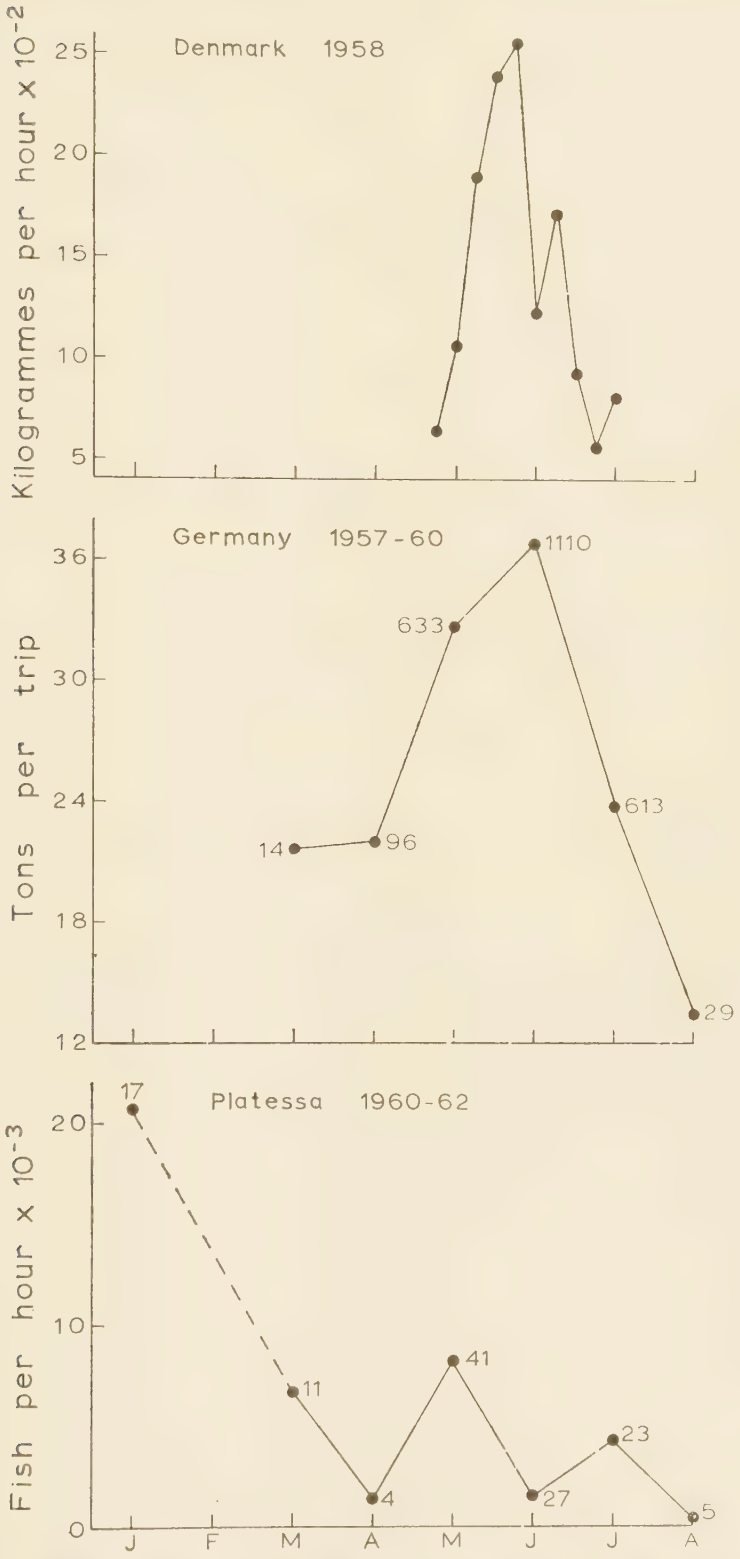


FIG. 22. *Seasonal changes in sand-eel catch per effort. The number at each point is number of trips (Germany) or number of hauls (R.V.* PLATESSA). *Values for Denmark – weekly: others – monthly.*

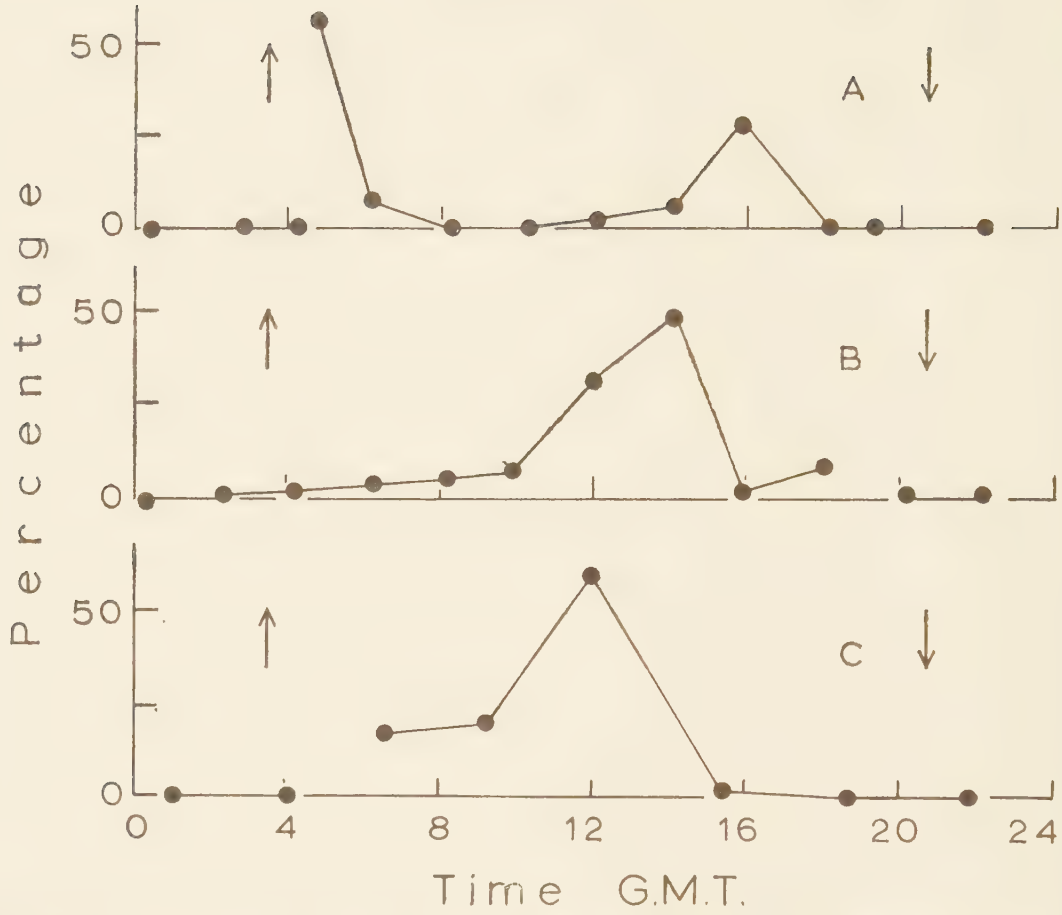


FIG. 23. *Diurnal variation in catches of sand eels. The arrows indicate sunrise* (↑) *and sunset* (↓); (*A*) 3–4 *June* 1958, (*B*) 11–12 *June* 1958; (*C*) 30 *April*–1 *May* 1961.

The non-availability of sand eels to capture in a bottom trawl at night could result from the fish burying themselves in the sand or swimming in midwater or at the surface at this time, and there is some evidence for each of these assumptions. Bertelsen and Popp Madsen (1958) caught more sand eels at night in a grab than during the day. Only one specimen was taken in a grab in daylight (number of hauls not stated), whilst twenty-two stations at night yielded thirteen sand eels. These authors also state that large numbers have been caught in midwater in a ring trawl at night. There have been several observations by my colleagues at this laboratory of sand eels seen on the surface at night, and many were caught by them with a hand net at the surface at night in early March in the Clay Deep area. These fish were mainly I-group *A. marinus* but there were also some I-group *A. lanceolatus*.

Attempts to throw further light on diurnal behaviour were unsuccessful. No sand eels were caught in midwater during twenty-four hour sampling with an Isaacs-Kidd net and a midwater sprat trawl on grounds where they were taken in abundance by a bottom trawl during daylight. Very few were caught in bottom-sampling devices such as dredges and grabs, and none were ever seen swimming at the surface by the present author. Cameron (1959 *a*), however, states that *A. lanceolatus* can be seen swimming at the surface from March–October (presumably in daylight). She also found that none were caught at night in a beach seine, which suggests that they were then buried, since they would be caught if they were swimming.

Diurnal variations in trawl catches have been described for most of the commercially important fish species in the north-east Atlantic area, and the latest work has been reported

FIG. 24. *Variation in daylight catches of sand eels by R.V.* PLATESSA *in* 1961.

at a recent ICES symposium (see section on 'Catch per unit effort: Behaviour and Diurnal Migration' in Gulland, ed., 1964). Briefly, it has been the most common experience that bottom trawl catches of most demersal species decrease at night, though in some cases the opposite has been found. Furthermore, it has been noted that flatfish in aquaria tend to remain quiescent during daylight and to become more active during darkness, though in the sea feeding takes place mainly during the day. The increased activity at night could explain the decrease in night catches, since the fish may then be swimming above the bottom.

Whether sand eels conform to this pattern is not known. They certainly feed near the bottom during the day, since they can be caught in a bottom trawl and their stomachs are generally full when caught. The presence of sand eels at the surface at night may be caused by bright lights from the ship; such responses have been described for other species (Woodhead 1963). Sonar work has not provided any evidence on diurnal behaviour changes in sand eels, since these fish have never shown up on *PLATESSA's* echo-sounder (Kelvin and Hughes MS 29, 30 kc/sec). Sometimes faint traces have been seen when sand eels have been caught, but these could have been caused by whiting which have also been taken at the same time. These results are in agreement with those of Bertelsen and Popp Madsen (1958), but Roessingh (1957) states that sand eels are 'plainly visible' on 'echogrammes'. They have also been described as having appeared on a sonar record during exploratory trawling off New England (Anon. 1958), and according to this report the record showed sand eels ascending to the surface at night. Sand eels do not possess an air-bladder, so reflection of sound waves would not be expected to be strong. Thus pulse frequency would be most important in determining whether or not these fish show up on sonar records.

## MORTALITY

There are several methods of estimating mortality in fish stocks. One of the simplest is to plot the logarithms of frequency of size- or age-groups, and in Figure 25 this has been done for the three sand-eel species. The ordinate is the abundance on all grounds on all cruises

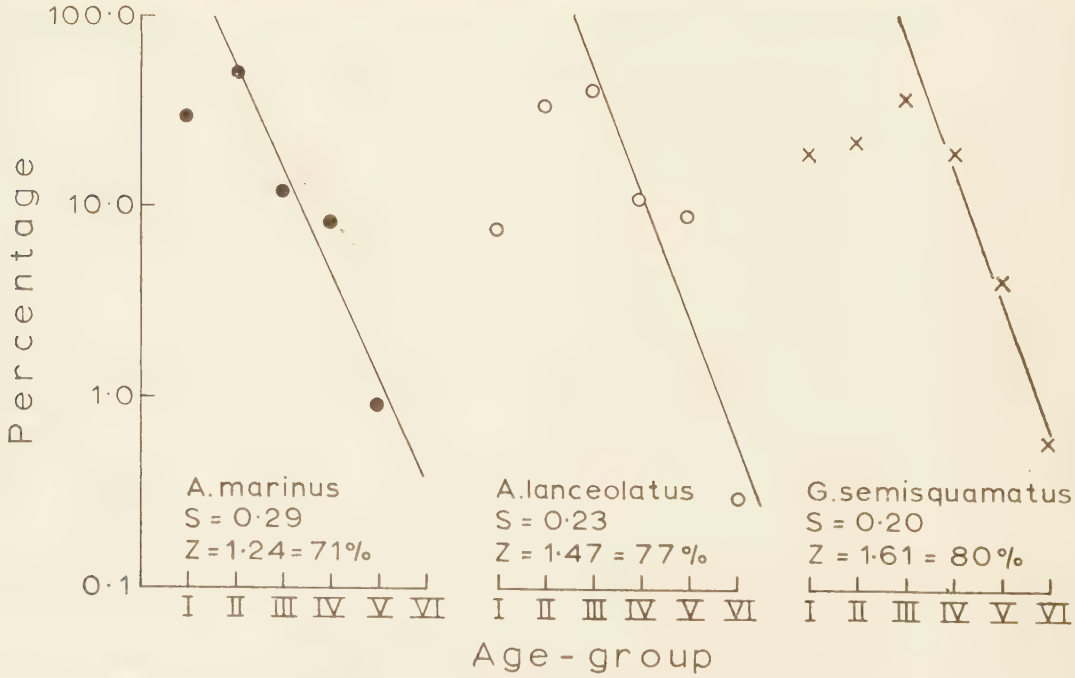


FIG. 25. *The average relative abundance* (1960–1962) *of each age-group in three species of sand eels, as caught by R.V.* PLATESSA. *S = survival; Z = total mortality.*

of *PLATESSA* (from 1960 to 1962), expressed as percentages. The curves correspond to the usual type, with an ascending left-hand limb and a descending right-hand limb. The ascending limb indicates that these age groups were not truly sampled, either because they had not yet fully recruited to the fishable stock or because they escaped capture due to mesh size; the descending limb represents mortality, provided that there are no such factors as emigration or avoidance of the gear, by the larger fish. A serious objection to the use of this method is that it is affected by the strength of year-classes, which tends to vary widely in sand eels, but the use of three years' data has helped to minimize this effect. The shape of the curve indicates that recruitment is a slow process in *A. lanceolatus* and *G. semisquamatus*, since mesh selection effects are unlikely, except in the I-group; with this age-group, escape through the meshes probably occurs early in the year, especially among *A. marinus* and *G. semisquamatus*. This may to some extent account for the relative scarcity of the I-group in *A. marinus*. The descending limbs of the curves have been fitted by regression, the slopes of which give the total mortality. They are very similar in all three species, lying between 70% and 80% per year. For each regression the survival, S, and mortality (as an instantaneous coefficient, Z, and as a percentage) are given, all values being annual ones. Bertelsen and Popp Madsen (1958) give figures for weekly catch per effort on the Southernmost Rough in 1958, and these data are plotted in Figure 26 as average weekly catch in weight per hour (log scale) for a period of ten weeks from 4 May to 12 July (all species). The slope of the right-hand limb (fitted by regression) gives a weekly reduction in weight of 21·7% (0·24 as an instantaneous coefficient) and hence a total coefficient of 2·4 for the whole 10-week period. Assuming no immigration or emigration this value represents the excess of mortality over growth. It is clearly much larger than the present estimates derived from

FIG. 26. *The abundance (as catch per effort) of sand eels on the Southernmost Rough from 4 May to 12 July* 1958 (*from Bertelsen and Popp Madsen* 1958).

age-composition data, and the reason could be that it is a measure of an intense local depletion over too short a time interval to permit much replenishment from peripheral concentrations. Since this fishery is carried out in a restricted area by a large number of boats (about 100 at that time), it can be assumed that a large part of the mortality is caused by fishing. The stocks are reduced very rapidly, and the fishery on each ground lasts for a few weeks only.

Another method of computing mortality is to compare the abundance (as catch per unit effort) of individual year-classes in successive years. This has been done in Table 9 for *A. marinus*, where the abundance (as mean number per one-hour haul from R.V. *PLATESSA*) of several year-classes is shown in 1960 and 1961. The data have been divided into three groups, corresponding to the three areas described previously. The Dogger area has been sampled more regularly and extensively than the other areas and it would be expected that these data would give the best estimates of mortality. Here, the mortality coefficient (Z) varies from 2·01 to 1·02, decreasing in the younger age-groups. The reason for this decrease could be that the 1960 abundance of the latter has been underestimated due to (a) mesh selection (in the I-group fish) or (b) prolonged recruitment. There was no evidence of (a) in the Dogger fish but (b) is a possibility, as explained previously. The mean value for Z for the Dogger fish is 1·39, a yearly mortality of 75%, which value is close to that derived from the data in Figure 25. The other grounds are somewhat anomalous because in several instances the abundance of year-classes increases from 1960 to 1961. The Dowsing data may be disregarded, since the 1960 abundance is based on a single haul. Those from the Norfolk Banks would seem to have a firmer basis, and here they suggest a local immigration, although mesh selection and recruitment may play a small part in the younger age-groups. If local migrations do occur, it could imply that the mortality estimate on the Dogger is overestimated due to emigration. In view of the known seasonal and diurnal changes in behaviour in sand eels, and the fact that the observations are based on relatively few research

Table 9. A. marinus. *Abundance (as mean number caught per one-hour haul) of year-classes in* 1960 *and* 1961, *as estimated from R.V. PLATESSA catches. (Number of hauls given in parentheses)*

| Year-class | Age-group | | Area | Abundance | | Mortality coefficient (Z) |
|---|---|---|---|---|---|---|
| | 1960 | 1961 | | 1960 | 1961 | |
| 1955 | V | VI | 1 | 82·4 (21) | 11·0 (24) | 2·01 |
| | | | 2 | 0 (1) | 19·2 (18) | ? |
| | | | 3 | 32·0 (14) | 15·7 (22) | 0·71 |
| 1956 | IV | V | 1 | 56·1 | 13·1 | 1·46 |
| | | | 2 | 25·0 | 4·9 | 1·63 |
| | | | 3 | 7·2 | 0·6 | 2·48 |
| 1957 | III | IV | 1 | 1 313·0 | 317·0 | 1·42 |
| | | | 2 | 361·0 | 184·3 | 0·67 |
| | | | 3 | 462·4 | 1 007·5 | ? |
| 1958 | II | III | 1 | 84·8 | 29·3 | 1·06 |
| | | | 2 | 55·0 | 90·8 | ? |
| | | | 3 | 91·1 | 389·8 | ? |
| 1959 | I | II | 1 | 813·0 | 294·3 | 1·02 |
| | | | 2 | 6 400·0 | 6 769·7 | ? |
| | | | 3 | 1 893·8 | 3 461·2 | ? |
| 1960 | 0 | I | 1 | – | 294·5 | – |
| | | | 2 | – | 2 421·7 | – |
| | | | 3 | – | 491·5 | – |

Area 1: Dogger
Area 2: Dowsing
Area 3: Norfolk Banks

hauls, it is likely that the mortality estimates indicate an order of magnitude, rather than an accurate estimate. Since sand eels occur in vast numbers, yet do not survive in large quantities beyond four years of age, it is clear that mortality must be large.

The numbers of *A. lanceolatus* and *G. semisquamatus* caught in 1960 were too small to permit assessments of abundance to be made.

## POSSIBLE EFFECTS OF THE SAND-EEL FISHERY ON OTHER SPECIES

The fishery for sand eels could affect other fish stocks in two main ways; firstly by the capture of undersized food fish in the small-meshed gear, and secondly by reducing food supplies for predators, since sand eels are eaten by many species of fish. In addition, food fish of legal size are caught, especially cod and whiting, but usually not in large quantities.

Sand eels were included in the list of species in Article 6 of the International Fisheries Convention of 1946, for whose capture small-meshed nets could be used, and these provisions have been repeated in the North-East Atlantic Fisheries Convention 1959 (Article 16). In each landing, it is permitted to include up to 10% by weight of undersized 'protected' species (i.e. those for which there are size limits, such as whiting, cod and plaice). This latter concession does not apply in the United Kingdom and, at the time of writing, it is illegal to land undersized protected fish here.

### BY-CATCH

Several factors have to be considered in assessing the so-called 'by-catch', that is, the amount of fish of species other than sand eels which is caught. The quantity of undersized fish landed may not be the same as that caught – it may be less, due to rejection at sea when too many are taken. On the other hand, it is possible that undersized fish will be deliberately sought (up to the 10% allowed) if sand eels are scarce. Thus the true by-catch must be assessed by research hauls, by analysis of landings and, if possible, by analysis of commercial catches at sea.

Research Hauls. The results of 157 hauls by R.V. *PLATESSA* during ten cruises in the south-west Dogger area are set out in Appendix Table 1, and also shown diagrammatically in Figure 27, the data being expressed in terms of numbers and weights. Most of the fish were measured at sea and the weights have been derived from weight/length records, chiefly from the Fish Stock Record (Anon. 1962). Data for lemon sole were kindly supplied by Dr. B. B. Rae. In other cases, for example herring, sprats, weevers and gurnards, the weight was estimated at sea. All hauls have been corrected to one hour's duration and the size limits used are those fixed in the original 1946 Convention, some having been changed since (e.g. whiting).

The top two sets of histograms in Figure 27 show the total composition of all hauls on each cruise, in terms of percentages of total numbers and weight. Four categories of fish are shown: sand eels, other unprotected species (fish for which there is no size limit), protected fish (all sizes), and undersized protected fish.

On seven of the ten cruises, sand eels greatly exceeded all other categories, both in numbers and weight, forming 78·8–99·3% and 60·0–91·4% respectively of the total catch. On the other three cruises sand eels did not predominate, due to herring and sprat in July 1960 and March 1961, and whiting in January 1961. The latter two cruises were outside the usual fishing season for sand eels in this area. The amount of undersized protected fish ranged from 0·1 to 5·9% (numbers) and 0·1 to 3·5% (weight) and was thus well below that allowed in the 1959 Convention.

Among the protected species, whiting always predominated, comprising on average 87·8% by number and 50·4% by weight of the total. Dabs were next in importance as far as numbers were concerned (6·1%) but not in weight, cod (38·1%) being more important.

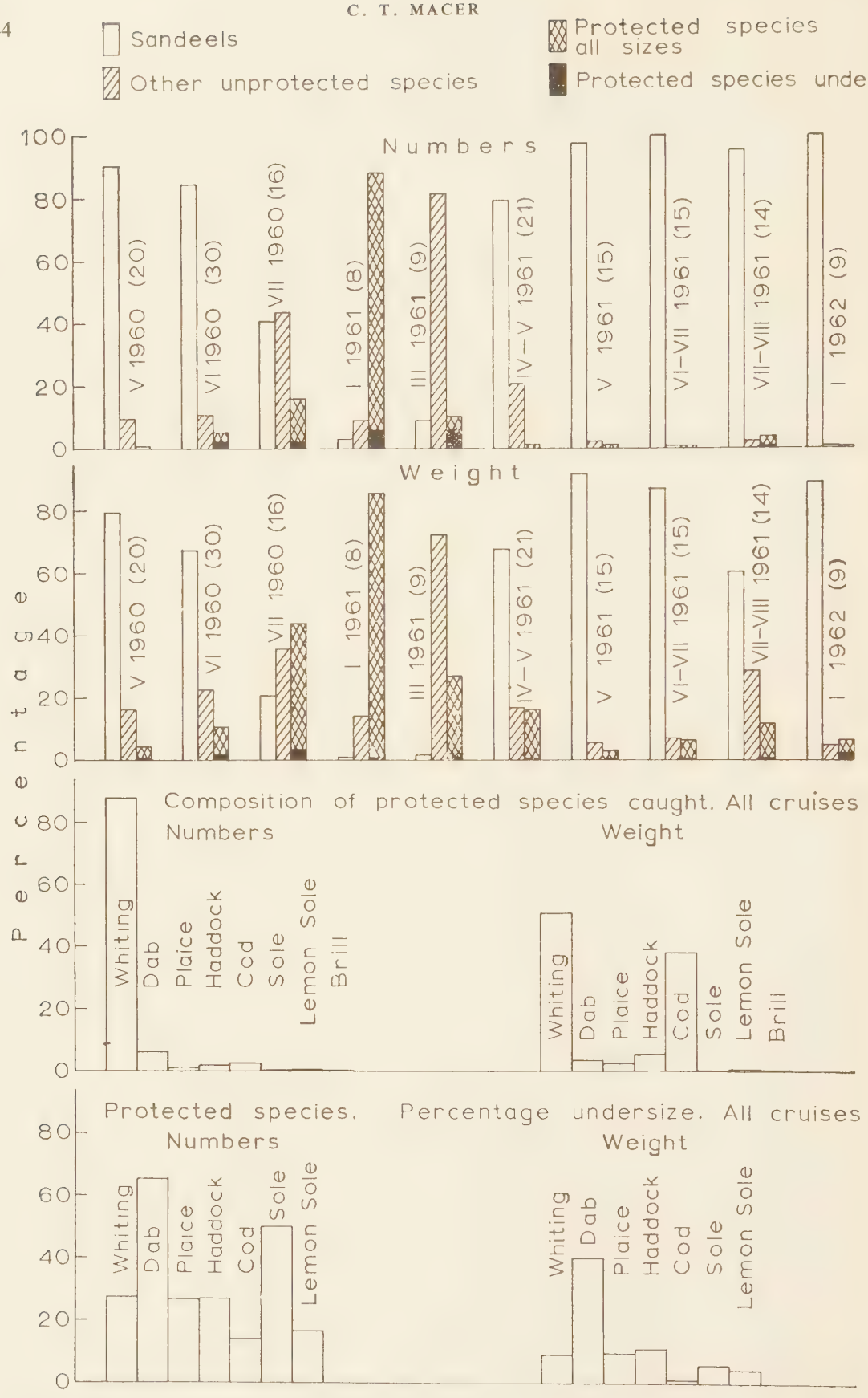


FIG. 27. *The composition of research haul catches by R.V.* PLATESSA *on each cruise. The month and year of each cruise is shown and the number of hauls is given in parentheses.*

N.B. *For each category of fish the histogram represents the percentage of the category in the*

The proportion of the protected species that was undersized varied widely. In whiting it ranged from 0 to 69·6% (numbers) and from 0 to 33·1% (weight), but on average the species having the greatest proportion of undersized fish was dabs (65·1% numbers and 40·0% weight). The amount of by-catch taken by the sand-eel trawl on sand-eel grounds is thus very small, confirming previous results (Roessingh 1957, Bertelsen and Popp Madsen 1958).

COMMERCIAL LANDINGS. The most detailed information on the by-catch from landings comes from Germany, and the data in Table 10, taken from information supplied by Lundbeck (1958 et seq.), show the by-catch from German sand-eel landings from 1957–1961. The figures do not include the landings from coastal fisheries, or those from deep-sea cutters landing in small ports (Lundbeck, personal communication). Somewhat higher values are given by Meyer-Waarden (1959, 1960). His analysis of samples of landings shows that sand eels form from 86·1 to 95·7% by weight of the total, and undersized protected species 0·5 to 0·8%; whiting comprised the bulk of protected species.

Table 10. *German sand-eel landings (from Lundbeck 1958 et seq.)*

| Year | Total landings (metric tons) | By-catch (metric tons) | By-catch percentage of total |
|---|---|---|---|
| 1957 | 25 596 | 72 | 0·3 |
| 1958 | 22 023 | 23 | 0·1 |
| 1959 | 21 278 | 30 | 0·1 |
| 1960 | 7 904 | 20 | 0·3 |
| 1961 | 4 267 | 32 | 0·8 |

Information on by-catch from Denmark and the Netherlands is shown in Table 11. It has been taken from an ICES report on mesh difficulties (Anon. 1960 *b*). For Denmark, sand eels form 98·4% of the total landings, and for the Netherlands 87·8%. Thus the results of analyses of landings confirm the findings from research hauls, viz., that the by-catch is small.

Table 11. *Landings in North Sea sand-eel fisheries*

| Country | Year | Total landings | Sand eels | Whiting | Dabs | Other species |
|---|---|---|---|---|---|---|
| Denmark | Average 1956–57 | 79 000 | 77 700 | 470 | 80 | 780 |
| Netherlands | 1957 | 3 700 | 3 250 | ← 80 → | | 370 |

In the data presented in Appendix Table 1 relating to hauls by R.V. *PLATESSA*, undersized whiting form 0·6% of the total weight. Sand-eel landings have been about 100 000 tons each year, which on this basis would mean the removal of 600 tons of undersized whiting each year. This estimate is larger than that given by an ICES group (Anon. 1960 *b*), who derived a value of 150–200 tons. The difference may be due to the fact that the value of 0·6% is based on hauls in the south-west Dogger area only, an area which is known to have a high density of whiting (though mainly in the deeper water) (Messtorff 1959). Both values are very small when compared with the estimated 2 000 tons of undersized whiting landed in the adult and young herring trawl fisheries in the North Sea and the Skagerrak/Kattegat (Anon. 1960 *b*). It was estimated that, had these whiting not been caught, the survivors would have represented about 9% of the total number of fish recruited annually to the adult whiting fisheries. Thus it may be concluded that destruction of undersized protected fish is not extensive in sand-eel fisheries.

## SAND EELS AS FOOD FOR OTHER FISH

In order to assess the effects of the sand-eel fishery in removing potential food for other fish, several factors must be considered, and the first of these is the extent to which sand eels are eaten by other fish. The species most important commercially which occur in the south-west Dogger area, and which are likely to feed on sand eels, are cod, whiting and plaice.

For cod Graham (1924) found that, in areas mainly to the north of the Dogger, the chief food items were haddock, herring, *Aphrodite* and *Nephrops,* sand eels not being important. Off Andenes and Iceland, Brown and Cheng (1946) found that sand eels were locally an important food of cod at certain times of the year, whilst off the east coast of Scotland, Brook (1885) found that they occurred in only 1% of cod stomachs. In an investigation on the food of various fish in the North Sea by Todd (1905, 1907), sand eels were again found to be of little importance to cod.

Jones (1954) concluded that the predominant food of Northern North Sea whiting larger than 21 cm is fish, usually small gadoids but occasionally sand eels in some areas; in fish below 21 cm sand eels were important but Crustacea formed the dominant food item. Todd (1905, 1907) did not find sand eels to be prominent as a food for whiting in the North Sea. The feeding of plaice in the North Sea including sand-eel areas was investigated by Todd (1914) and although sand eels did occur, the chief foods were Mollusca and Annelida. In the Irish Sea, in an investigation by Jones (1952), Mollusca and Crustacea were found to be the chief food of plaice.

In the present investigation representative samples of stomachs were examined from the protected fish species caught. It was found that in the areas where sand eels were concentrated, whiting above about 20 cm and cod were feeding largely on them; in other areas sand eels were less important as food. The few plaice which were caught were not, in general, taking sand eels. In many cases, the sand eels which were taken from the stomachs were still alive and had clearly been swallowed very recently, possibly in the trawl. This was especially true of cod and in such circumstances trawl-caught fish may give a false picture, in that the trawl may disturb the sand eels, when normally they could escape predation by burrowing.

If sand eels are actively sought after by other fish it would be expected that large numbers of predators would be caught on sand-eel grounds. The construction and rig of the sand-eel trawl is such that it is not suitable for the capture of flatfish, so the fact that few are caught does not mean that few are present. This is not true of roundfish, however, and so the small amounts caught would indicate that the density is low. Whiting and cod have been caught with this gear in fairly large quantities by R.V. *PLATESSA*. Thus, for example, 40 cod (45-minute tow) were caught on the Indefatigable Bank and 36 cod (one-hour tow) off the Swarte Bank. In general, however, large catches such as these were exceptional. The areas where sand eels are abundant are not the main areas of cod abundance in the North Sea. An analysis of monthly catch of cod per hundred hours' fishing for each statistical rectangle shows that the greatest density occurs farther to the north-west than the sand-eel grounds on the south-west Dogger. Abundance of cod is high, however, from January to April in the statistical squares which include the south-west Dogger, and this is probably due to aggregation on the Flamborough spawning ground (Graham 1924).

To summarize, it seems that both whiting and cod will at times eat sand eels, especially in areas where the latter are abundant. Since sand eels occur in such vast numbers it would be surprising if this were not so, unless the predators had a positive dislike for them. This is unlikely since sand eels, live or artificial, are a well-known bait for cod and other species. Both cod and whiting take a variety of other food organisms and it is doubtful whether a reduction in sand eel numbers would seriously affect them.

This leads to another important point – the extent to which sand-eel numbers are reduced by the fishery. Owing to the long distance of the Dogger and Norfolk Banks grounds from the continental ports (for example, 300 nautical miles approximately from Esbjerg), it is necessary for the boats to fill their holds quickly in order to make the trip profitable. In addition, the fish must be transported as quickly as possible before they decay, since no ice is used. (Dutch fishermen have, however, used chemical preservatives.) A high catching

rate is thus essential, and for Danish boats in 1958 it was estimated that the minimum economic rate was one ton (about twenty-five baskets) per hour (Bertelsen and Popp Madsen 1958). The profitability or otherwise of the fishery is to a large extent governed by the world prices of fishmeal, especially Peruvian, so these will have an effect on fishing strategy, and may determine, for example, the minimum economic catching rate.

The most relevant fact is that when sand-eel boats have left a ground sand eels still remain at a high density. For example, in July 1961 R.V. *PLATESSA* was able to catch $3\frac{1}{2}$ baskets (5 898 fish) per hour on the Southernmost Rough, although the commercial fishery there had ended. Again, in July 1962 on the same ground, 3 088 fish/hour were caught though no sand-eel boats were present. These densities of sand eels, though not commercially profitable, would nevertheless probably provide ample food for predators. In addition to sand eels, other fish which are preyed upon, such as sprats and young herring, are abundant in the area in summer, particularly around the Norfolk Banks.

# CONCLUSIONS

THE present work has not revealed anything which would suggest that the sand-eel fishery has an adverse effect on other fish stocks. The destruction of undersized food fish is very small, especially when compared with that in other industrial fisheries, and with the quantity of adult food fish landed in non-industrial fisheries. Sand eels occur commonly in the stomachs of many species at certain times in some localities, but have rarely proved to be the most important food organism in the published accounts of stomach analyses. Thus even if sand eels were completely fished out there might still be no detrimental effect on other species' food supplies. As has been seen, however, the fishery ceases (due to economic factors) when there is still a high density of sand eels present, so there seems to be no possibility, at the present time; of a lack of sand eels as food for predators.

An important factor to be considered is that if the boats were not fishing for sand eels they would be fishing for something else, probably plaice, cod or sole. According to the literature there have been as many as six hundred boats fishing for sand eels in the North Sea and, although they are mainly small vessels, their combined fishing effort must be considerable. Thus the sand-eel fishery must surely 'relieve the pressure' on other fish stocks to some extent, provided the fishing fleets are not enlarged so as to exploit both sand eels and non-industrial stocks, that is, they cease to be alternatives.

While it is not possible to make detailed predictions about the future yield of the fishery, a few broad conclusions can be drawn. Since the fish are short-lived and the fishery depends on the first few age groups, the effect of variations in year-class strength (that is, the success of each spawning) will be quickly felt by the fishery. Similarly, if the stocks were reduced to a low level they could quickly recover, provided there is no relation between stock and recruitment. Fecundity of *A. marinus* is high compared with the weight of the fish; using the data on fecundity and weight/length, the number of eggs per gramme weight of fish is 779. For herring ('Downs' stock) the comparable figure is about 212 (Bridger 1961, Figure 3, p. 11), for plaice between about 140 and 170 (Simpson 1951), and for haddock about 143 (Raitt 1933). Similar data for various species are given by Simpson in Graham ed. (1956); the data which he quotes for sand eels (from Fulton 1891) refer to *A. lancea*. In some other fish species the fecundity is much higher than in *A. marinus* (e.g. ling – 1 500 per gramme, Fulton 1891).

The relatively high fecundity of *A. marinus*, coupled with the very high densities of fish present, accounts for the large numbers of larvae of this species (Macer 1965). Provided the stock size is not reduced to such a level as to influence subsequent recruitment, the fishery would not seem to be doing serious damage to the sand-eel populations.

# SUMMARY

1. FIVE species of sand eels have been recorded from the North Sea – *Ammodytes marinus* Raitt, *A. lanceolatus* Lesauvage, *Gymnammodytes semisquamatus* (Jourdain), *A. lancea*

Cuvier and *A. immaculatus* Corbin. The first three species are common offshore and, in the area investigated, they were concentrated on the south-western edge of the Dogger Bank and, except for *G. semisquamatus*, on the tops of the Norfolk Banks. *A. marinus* comprised 94·5% of all sand eels caught and it is on the large concentrations of this species that the fishery depends.

2. On the Dogger Bank growth rate of sand eels is higher than on the Norfolk Banks and Dowsing areas. Marked variations in annual growth and year-class strength were found to occur, especially in *A. marinus*. The fish are short-lived, the oldest found being IX-group, *A. marinus*; VIII-group, *A. lanceolatus*; and VII-group, *G. semisquamatus*.

3. The weight/length relationship corresponds to the usual one found in fish, i.e. $W = aL^n$. The exponent was 3·068, *A. marinus*; 2·928, *A. lanceolatus*; and 3·476, *G. semisquamatus*.

4. Data on maturity confirm previous findings that *A. marinus* is a winter spawner, and *A. lanceolatus* and *G. semisquamatus* summer spawners. First maturity is reached at one or two years of age, depending on the species. Spawning areas of all three species were found in the Southern Bight and Dowsing areas. A feature of sex ratio analyses was the preponderance of males, at spawning time only, in *A. marinus*. Fecundity estimates were made for the latter species only and the number of eggs was found to be proportional to a power (3·055) of the length of the fish. Egg measurements showed that *A. marinus* has a short spawning period, and *A. lanceolatus* and *G. semisquamatus* prolonged ones.

5. Stomach content analyses show that *A. marinus*, *A. lancea* and *G. semisquamatus* are plankton feeders (taking chiefly copepods), whilst *A. lanceolatus* and probably *A. immaculatus* are, except for the juveniles, predators on other fish, often sand eels, though not their own species.

6. The industrial fishery for sand eels started in 1953. Denmark, Germany, Norway and the Netherlands have taken part and they fish along their own coasts and also in the south-west Dogger area.

7. Annual landings have been about 100 000 tons or more, though in 1962 and 1963, sharp increases led to a figure of 183 863 tons. Over 80% of the total is usually taken by Denmark. The fishery is seasonal (March–August). The fish cannot be caught at night in a bottom trawl.

8. Mortality estimates indicate a value of between 70 and 80% annually.

9. The amount of undersized protected species in 157 research hauls with the sand-eel trawl varied between 0·1 and 3·5% by weight.

10. The possible effects of the fishery on stocks of sand eels and other fish are discussed.

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Appendix Table 1. *By-catch data. All PLATESSA hauls*

| Cruise and dates | No. of hauls | SAND EELS | | | | WHITING | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Total | | Undersized | | | |
| | | No. | % of All species | Wt (kg) | % of All species | No. | Wt (kg) | No. | % | Wt (kg) | % |
| *PLATESSA* VI/60 5.5.60–12.5.60 | 20 | 120 142 | 90·2 | 1 368·18 | 79·7 | 731 | 53·34 | 151 | 20·7 | 2·91 | 5·5 |
| *PLATESSA* VIII/60 9.6.60–15.6.60 | 30 | 36 431 | 84·5 | 1 021·96 | 67·1 | 2 093 | 118·35 | 858 | 41·0 | 24·40 | 20·6 |
| *PLATESSA* IX/60(2) 1.7.60–5.7.60 | 16 | 4 946 | 40·5 | 116·05 | 20·5 | 1 638 | 100·19 | 108 | 6·6 | 6·87 | 6·9 |
| *PLATESSA* I/61 13.1.61–21.1.61 | 8 | 42 | 2·9 | 0·69 | 0·4 | 1 234 | 115·55 | 62 | 5·0 | 1·08 | 0·9 |
| *PLATESSA* V/61 17.3.61–26.3.61 | 9 | 1 297 | 8·8 | 12·09 | 1·2 | 1 142 | 58·17 | 691 | 60·5 | 12·59 | 21·6 |
| *PLATESSA* VII/61 29.4.61–5.5.61 | 21 | 134 071 | 78·8 | 1 916·41 | 67·3 | 1 492 | 167·75 | 106 | 7·1 | 2·32 | 1·4 |
| *PLATESSA* IX/61 23.5.61–30.5.61 | 15 | 102 722 | 97·2 | 1 182·04 | 91·4 | 970 | 37·86 | 322 | 33·2 | 7·86 | 20·8 |
| *PLATESSA* XI/61 27.6.61–4.7.61 | 15 | 88 047 | 99·3 | 1 040·47 | 86·8 | 343 | 36·85 | 17 | 5·0 | 0·48 | 1·3 |
| *PLATESSA* XIII/61 27.7.61–3.8.61 | 14 | 29 003 | 94·5 | 688·00 | 60·0 | 895 | 105·35 | 0 | 0 | 0 | 0 |
| *PLATESSA* I/62 3.1.62–10.1.62 | 9 | 350 820 | 99·3 | 1 109·74 | 88·9 | 1 259 | 52·78 | 876 | 69·6 | 17·46 | 33·1 |
| TOTALS | 157 | 867 521 | 91·0 | 8 455·63 | 66·4 | 11 797 | 846·19 | 3 191 | 27·1 | 75·97 | 9·0 |
| Mean per one-hour haul | – | 5 526 | | 53·86 | | 75 | 5·39 | 20 | | 0·48 | |
| Protected species – % composition | | | | | | 87·8 | 50·4 | | | | |

% = Percentage of that individual species, except where stated.

Appendix Table 1. *By-catch data. All PLATESSA hauls* – cont.

| DAB | | | | | | PLAICE | | | | | | HADDOCK | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total | | Undersized | | | | Total | | Undersized | | | | Total | | Undersized | | | |
| No. | Wt (kg) | No. | % | Wt (kg) | % | No. | Wt (kg) | No. | % | Wt (kg) | % | No. | Wt (kg) | No. | % | Wt (kg) | % |
| 47 | 4·59 | 20 | 42·6 | 1·01 | 22·0 | 7 | 1·62 | 3 | 42·9 | 0·30 | 18·5 | 2 | 1·64 | 0 | – | – | – |
| 17 | 1·16 | 11 | 64·7 | 0·54 | 46·6 | 2 | 1·50 | 0 | – | – | – | 15 | 5·62 | 7 | 46·7 | 0·86 | 15·3 |
| 78 | 5·02 | 59 | 75·6 | 2·85 | 56·8 | 2 | 2·17 | 0 | – | – | – | 154 | 53·82 | 62 | 40·3 | 8·92 | 16·6 |
| 25 | 0·38 | 24 | 96·0 | 0·27 | 71·1 | 3 | 0·65 | 0 | – | – | – | 33 | 9·75 | 0 | – | – | – |
| 205 | 12·47 | 129 | 62·9 | 4·87 | 39·1 | 87 | 19·98 | 24 | 27·6 | 1·95 | 9·8 | 0 | – | 0 | – | – | – |
| 43 | 4·63 | 26 | 60·5 | 2·73 | 59·0 | 3 | 1·96 | 0 | – | – | – | 34 | 10·02 | 0 | – | – | – |
| 3 | 0·10 | 3 | 100·0 | 0·10 | 100·0 | 3 | 0·90 | 0 | – | – | – | 1 | 0·31 | 0 | – | – | – |
| 7 | 0·53 | 4 | 57·1 | 0·17 | 32·1 | 2 | 0·52 | 0 | – | – | – | 0 | – | 0 | – | – | – |
| 100 | 8·59 | 56 | 56·0 | 2·41 | 28·1 | 11 | 1·74 | 5 | 45·5 | 0·51 | 29·3 | 18 | 7·94 | 0 | – | – | – |
| 295 | 17·34 | 202 | 68·5 | 6·95 | 40·1 | 26 | 5·07 | 7 | 26·9 | 0·69 | 13·6 | 0 | – | 0 | – | – | – |
| 820 | 54·81 | 534 | 65·1 | 21·90 | 40·0 | 146 | 36·11 | 39 | 26·7 | 3·45 | 9·6 | 257 | 89·10 | 69 | 26·9 | 9·78 | 11·0 |
| 5 | 0·35 | 3 | | 0·14 | | 1 | 0·23 | <1 | | 0·02 | | 2 | 0·57 | <1 | | 0·06 | |
| 6·1 | 3·3 | | | | | 1·1 | 2·2 | | | | | 1·9 | 5·3 | | | | |

Appendix Table 1. *By-catch data. All PLATESSA hauls* – cont.

| Cruise and dates | No. of hauls | COD | | | | | | LEMON SOLE | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Total | | Undersized | | | | Total | | Undersized | | | |
| | | No. | Wt (kg) | No. | % | Wt (kg) | % | No. | Wt (kg) | No. | % | Wt (kg) | % |
| *PLATESSA* VI/60 5.5.60–12.5.60 | 20 | 12 | 11·21 | 2 | 16·7 | 0·30 | 2·7 | 1 | 0·18 | 0 | – | – | – |
| *PLATESSA* VIII/60 9.6.60–15.6.60 | 30 | 32 | 36·83 | 3 | 9·4 | 0·44 | 1·2 | 1 | 0·14 | 1 | 100 | 0·14 | 100 |
| *PLATESSA* IX/60(2) 1.7.60–5.7.60 | 16 | 54 | 78·56 | 8 | 14·8 | 1·28 | 1·6 | 19 | 8·79 | 1 | 5·3 | 0·16 | 1·8 |
| *PLATESSA* I/61 13.1.61–21.1.61 | 8 | 2 | 6·05 | 0 | – | – | – | 1 | 0·01 | 1 | 100 | 0·01 | 100 |
| *PLATESSA* V/61 17.3.61–26.3.61 | 9 | 40 | 184·76 | 6 | 15·0 | 0·77 | 0·4 | 1 | 0·20 | 0 | – | – | – |
| *PLATESSA* VII/61 29.4.61–5.5.61 | 21 | 163 | 272·89 | 8 | 4·9 | 0·98 | 0·4 | 4 | 1·57 | 0 | – | – | – |
| *PLATESSA* IX/61 23.5.61–30.5.61 | 15 | 1 | 0·21 | 1 | 100 | 0·21 | 100 | 0 | – | 0 | – | – | – |
| *PLATESSA* XI/61 27.6.61–4.7.61 | 15 | 22 | 37·41 | 2 | 9·1 | 0·22 | 0·6 | 0 | – | 0 | – | – | – |
| *PLATESSA* XIII/61 27.7.61–3.8.61 | 14 | 32 | 7·95 | 12 | 37·5 | 1·51 | 19·0 | 2 | 0·26 | 1 | 50·0 | 0·06 | 23·1 |
| *PLATESSA* I/62 3.1.62–10.1.62 | 9 | 17 | 3·46 | 10 | 58·8 | 0·66 | 19·1 | 1 | 0·10 | 1 | 100 | 0·10 | 100 |
| TOTALS | 157 | 375 | 639·33 | 52 | 13·9 | 6·37 | 1·0 | 30 | 11·25 | 5 | 16·7 | 0·47 | 4·2 |
| Mean per one-hour haul | | 2 | 4·07 | <1 | | 0·04 | | <1 | 0·07 | <1 | | 0·003 | |
| Protected species —% composition | | 2·8 | 38·1 | | | | | 0·2 | 0·7 | | | | |

Appendix Table 1. *By-catch data. All PLATESSA hauls* – cont.

| ALL PROTECTED SPECIES | | | | | | | | | | OTHER UNPROTECTED SPECIES | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total | | | | Undersized | | | | | | | | | |
| No. | % all Spp. | Wt (kg) | % all Spp. | No. | % Prot. Spp. | % all Spp. | Wt (kg) | % Prot. Spp. | % all Spp. | No. | % all Spp. | Wt (kg) | % all Spp. |
| 801 | 0·6 | 72·77 | 4·2 | 176 | 22·0 | 0·1 | 4·52 | 6·2 | 0·3 | 12 201 | 9·2 | 276·35 | 16·1 |
| 2 160 | 5·0 | 163·60 | 10·7 | 880 | 40·7 | 2·0 | 26·38 | 16·1 | 1·7 | 4 532 | 10·5 | 337·20 | 22·2 |
| 1 947 | 15·9 | 248·58 | 43·9 | 240 | 12·3 | 2·0 | 20·11 | 8·1 | 3·5 | 5 324 | 43·6 | 201·90 | 35·6 |
| 1 298 | 88·2 | 132·39 | 85·6 | 87 | 6·7 | 5·9 | 1·36 | 1·0 | 0·9 | 132 | 8·9 | 21·51 | 14·0 |
| 1 475 | 10·0 | 275·58 | 26·8 | 850 | 57·6 | 5·8 | 20·18 | 7·3 | 2·0 | 11 928 | 81·2 | 742·68 | 72·0 |
| 1 739 | 1·0 | 458·82 | 16·1 | 140 | 8·1 | 0·1 | 6·03 | 1·3 | 0·2 | 34 266 | 20·2 | 474·45 | 16·6 |
| 978 | 0·9 | 39·38 | 3·1 | 326 | 33·3 | 0·3 | 8·17 | 20·8 | 0·6 | 1 938 | 1·9 | 72·00 | 5·5 |
| 374 | 0·4 | 75·31 | 6·3 | 23 | 6·2 | 0·03 | 0·87 | 1·2 | 0·1 | 261 | 0·3 | 83·60 | 6·9 |
| 1 058 | 3·5 | 131·83 | 11·5 | 74 | 7·0 | 0·2 | 4·49 | 3·4 | 0·4 | 626 | 2·0 | 327·00 | 28·5 |
| 1 599 | 0·5 | 79·04 | 6·3 | 1 096 | 68·5 | 0·3 | 25·86 | 32·7 | 2·1 | 758 | 0·2 | 60·00 | 4·8 |
| 13 429 | 1·4 | 1 677·30 | 13·2 | 3 892 | 29·0 | 0·4 | 117·97 | 7·0 | 0·9 | 71 966 | 7·6 | 2 596·69 | 20·4 |
| 86 | | 10·68 | | 25 | | | 0·75 | | | 458 | | 16·54 | |

% = Percentage of that individual species, except where stated.
Also caught – 3 brill, 4 soles.

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